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THE WASP, *VESPULA SYLVESTRIS* SCOPOLI: FEEDING, FORAGING AND COLONY DEVELOPMENT.

By M. V. BRIAN and A. D. BRIAN.
(*Zoology Department, Glasgow University.*)

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With 4 text figures

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1. Introduction.

In 1947 the initial stages of nest-construction by two queen *Vespula sylvestris* Scopoli were observed, and have been recorded (Brian and Brian, 1948). Both queens died very early in the work, but in the two succeeding years even more favourable opportunities occurred, and further stages in brood growth have been studied. The times of emergence of queens of this species in the four years 1947–1950 have been related to the prevailing maximum temperatures in April and May (fig. 1)[1]. The ten days delay in 1947 could reasonably be attributed to the cooler preceding period.

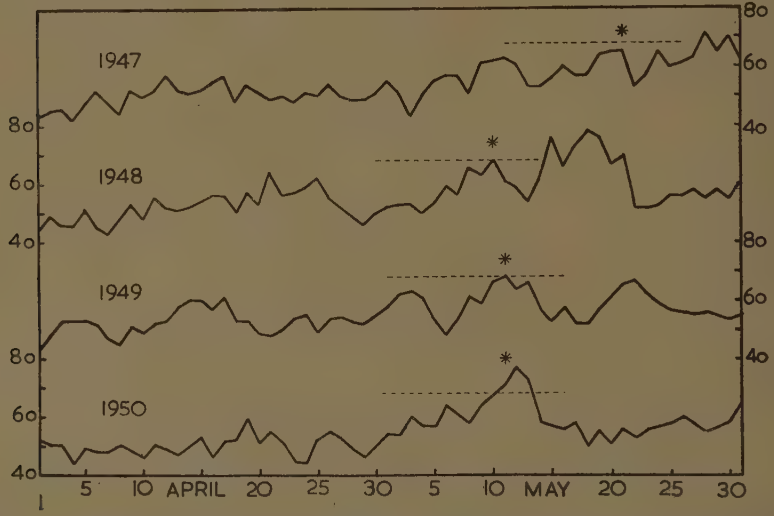

Fig. 1.—Maximum temperature (Fahrenheit) for April and May, and first emergence of *V. sylvestris* (*), 1947–1950.

Of six nests in 1948, two were in a caravan inhabited by the authors and four were in specially designed holes. These were 9 inches deep, and 6 inches in diameter, dug in banks and covered with flat stones in such a way as to leave a small space for the wasp to move in and out. Nests were suspended either from the underside of the stone, or from grass stems round the rim of the hole. In 1949 a further four nests were found in the queen stage of development (that is, with no workers), two in the caravan, one in a canvas bag, and another in one of the specially designed holes.

The minimum requirement for nest-site in this species appears to be an overhanging projection from which to suspend the nest and which, no doubt, affords it some shelter from rain. The character of the support and its height vary enormously. Out of a total of 19 nests, six have been subterranean, but not down long burrows or holes, five have been in the caravan at various heights up to 10 feet, three in the roof of a cottage (about 12 feet from the ground), three in overhanging projections of a bank, probably abandoned rabbit scrapes, one in a canvas bag, and one under a mattress indoors. In this respect the species seems to bridge the gap in a series of habitat types descending from the arboreal *Vespula norwegica* (Fabricius) to the subterranean *rufa* (Linnaeus), *germanica* (Fabricius) and *vulgaris* (Linnaeus).

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[1] For the temperature and other weather data we are indebted to the Burgh Surveyor, Helensburgh.

Of the ten *sylvestris* nests found in 1948 and 1949, four which were watched from the start gave confirmation of the general procedure outlined in an earlier paper (*loc. cit.*). The other nests were not found until four or five days after initiation. In the two years, seven colonies were studied with varying intensity, C, D, E, F and H in 1948, and I and J in 1949 (these have been listed with a few relevant facts in Table I)[2]. The three other colonies failed to progress very far : one was destroyed by a small mammal, and the other two lost their queens on the second and fifth days.

Of the seven nests, only one achieved an appreciable worker population. In one the queen was accidentally killed ; in the others she disappeared, from causes unknown, although in most cases associated with a general weakness of flight and lack of attention to brood which could conceivably have led to flying accidents or predation. Two of these nests showed queen replacement. This took place twice in nest C after the original queen (marked with cellulose paint) had successfully killed an early invader, and there were three queens successively in nest H. In fact, replacement was surprisingly common, but in none of the cases observed did it enable the nest to continue successfully. It would be interesting to know whether the usurpers have earlier built a nest of their own and had it destroyed or whether they represent an incipient parasitic subspecies (see, for example, Richards, 1927). Cumber (1949) found that wild bees of the genus *Bombus*, searching for nest-sites later than usual, were parasitized.

2. COLONY DEVELOPMENT.

In a few of the nests (C, E, H and J) built in such a way that they could be inverted, it was possible to record the brood sequence by making a cell-map daily (these details are filed with the tables). As brood is not moved about at all, this perfectly static individual localization is a great boon in population work. In nests not so conveniently placed, only the major events such as the first pupa or the first worker could be recorded (D, F and I), but in all seven the cells and envelopes were counted frequently.

Two larval stages were distinguished, an " inward-facing " and an " outward-facing." The newly-hatched larva is cemented to the cell near its base, and faces outwards, that is, along a radius away from the centre of the comb. After two instars in this position it moults,[3] and this time, instead of refixing, it remains free to move. Subsequently it holds itself in the cell by means of lateral flanges, and turns to face inwards. But occasionally they were found facing outwards, and once a larva, when presented with food, moved a full circle ! It has been suggested that orientation in this stage results from a thigmotatic reaction to the curvature of the cell, which fits their form better in one direction than in the other (Duncan, 1939). The position of the fixed stages is presumably the consequence of a definite orientation of the queen during oviposition as in the honey-bee, although no record or observation of this is known to us.

---

[2] **All the tables referred to in this paper, including those forming the Appendix, have been deposited in the Archives established in the British Museum (Natural History).**

[3] By marking with paint it was found that they lost their mark at the same time as they turned round.

Besides recording brood and nest condition, it was possible in most cases to obtain some idea of the amount of protein food given to the larvae. All the larvae are given masticated flies (adult Diptera are the usual food), which they digest to a great extent externally. The black chitinous residues chiefly formed by the larger larvae are flicked away from the mouth and fall out of the nest. By collecting these pellets in a dish their daily and sometimes hourly variation in number and weight was determined.

(a) *Details of Two Representative Colonies.*

In colony J, records of the early stages are complete (see fig. 2 and Appendix Table IV). Eggs were laid in each cell as soon as prepared (strictly at first, less so later), and by the fifth day there were 15 cells, each with an egg. This number of eggs was never again exceeded and only once equalled, for on the sixth day young larvae appeared in the central cells and, although new cells and new eggs were continually added (rather irregularly), the rate of addition was slower than in the first few days with the result that the egg population as a whole declined. On the 11th day inward-facing larvae first made their appearance, and pellets were collected. Pupae were formed on day 14 and their numbers rose to a maximum of five on Day 18. They were produced from the five earliest eggs, which thus showed maximum fertility and survival.

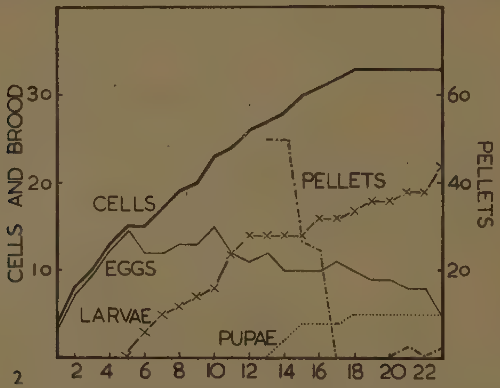

Fig. 2.—Brood details and pellet production for nest J. Abscissa: days from start of nest. Ordinates: numbers of cells, brood and pellets.

With a constant egg-inflow there should be, ideally, a constant outflow of adults at the same rate, and the number of individuals in each ontogenetic stage should be proportional to the duration of that stage. It is clear, however, that even if the egg input had remained at its initially high rate, output could not succeed in equalling it unless the vast amount of food needed for body-building could be collected and assimilated. Although initially the larval demand for food appears to have received much attention (see pellet production), it did not continue to do so, apparently through no fault of the climate (see Appendix Table VI), and a general retardation of larval growth-rate, shown by a prolongation in each instar, followed the formation of pupae. During this phase also, it was noticeable that cells contained eggs for much longer than hitherto, a fact which could result from one or all of three things, namely, infertility and replacement within the census period, cannibalism and similar replacement, or failure to hatch without any replacement. These alternatives will be discussed later.

Perhaps these failings, egg-persistence and larval growth retardation, may both result from the queen's failure to continue effective foraging, itself perhaps a consequence either of an independent physiological change, or of a specific response to the presence of pupae.

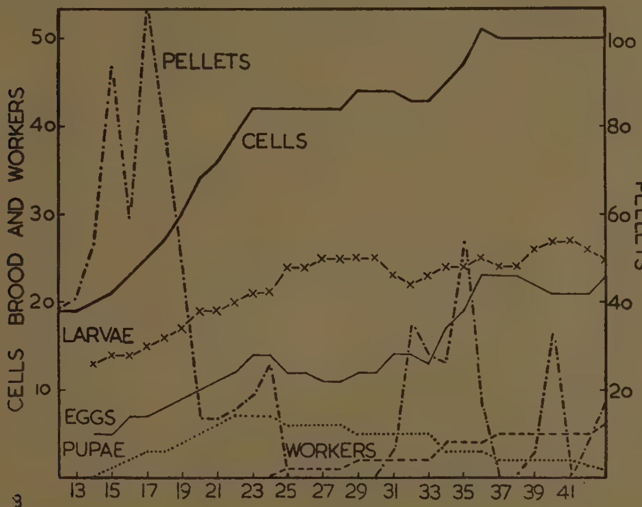

Fig. 3.—Brood details and pellet production for nest E. Abscissa: days from start of nest. Ordinates: numbers of cells, brood, workers and pellets.

With colony E (Appendix Table II and fig. 3) observations extend to the 43rd day, but do not begin, except for cells and envelopes, until Day 14. From then for about ten days the similarity to J is striking except for the minor difference that cell construction had a second maximum about the 19th day. The retardation of brood changes is well shown by the history of the first seven individuals: laid in two days they pupated over a period of six days and emerged as workers over a period of 18 days. One failed to emerge, but a success of six out of seven seems very creditable.

These six workers began appearing on the 25th day and, following this, more cells were constructed and more flies brought in. From the 30th day onwards quite a number of small larvae entered their final instar, although a number also died and were replaced by eggs—usually on the same day. In spite of this revival no more pupae were formed, and several of the older third instar larvae died and were either eaten or carried from the nest. Oviposition is difficult to estimate owing to the possibility of unknown egg replacements, but, when relaying in the first cells as the workers emerged is taken into account, it appears to have been maintained at quite a high rate. This colony, which thus showed signs of returning activity, due to the workers, might have reached maturity but for the unexplained loss of its queen.

(b) *Comparison of Seven Colonies.*

Envelopes.—The queens varied a good deal in the number of envelopes they made: all began at least two, but queen I began five (Tables II and III).

Quite frequently the later ones were left unfinished and it was also common to begin another before the previous one was complete. Envelope-making was the first activity which the queens abandoned. Thus E and F stopped about the time when their first larvae were appearing. Queen C continued even when she had pupae as did I, the only successful one. By the 13th day I had 4 complete envelopes and the nest temperature was being maintained 3–6° C. above that of the surrounding air.

Even in these "better" nests (C and I), there was an appreciable lull between the queen's work and that of the workers, although these latter usually began to apply pulp on the second or third day after their emergence. In nest I this lull lasted eleven days (Day 13 to Day 24). At first the workers spent a considerable time buttressing the suspension—still the single sheet made by the queen on her first day—which was by this time unable to prevent a dangerous swaying of the enlarged nest. Sheets of pulp were applied at right-angles to the original support, connecting the outer envelope with the superstratum. After this the inner envelopes were broken down, from near the top to the bottom, and first converted into cells, but later into outer envelopes. Progress has been tabulated (Table III), and shows that never more than three and often only two envelopes were retained at any particular time. This transference outside was first noticed on Day 33 when a worker was seen to emerge from the nest with pulp which she had not previously carried in[4].

On the 42nd day work on the second tier of cells began, before the first had reached its maximum size. This feature of design enabled full use of the inch or more of space left below the top tier by the removal of envelopes.

Workers applied pulp in the same way as the queen, but were less strict about envelope spacing, and frequently ran one into another. Individuals did not resort to specific parts of the envelope, working these repeatedly, but, as far as could be judged, added their pulp at any convenient place.

Cells.—The queens continued making cells for much longer than envelopes and, in fact, in some cases (D, to a less degree C), did not actually stop. In E, F, H and J, the queen halted for several days after substantial pupation had been achieved, at levels respectively of 42, 37, 31 and 33 cells, and in two of these (E and F) construction was resumed with the appearance of workers. All queens agreed in showing a rapid initial construction with a slackening between the fifth and tenth days. This was associated with, and perhaps

[4] The nest is always entered for a few seconds on returning even if subsequent application is external.

related to, the appearance and growth of larvae. In some colonies a second maximum cell construction rate, due solely to the queen, was detectable. This was especially noticeable in E, where it centred about Day 18, and in C about day 15, in both cases beginning at about the same time as pupation.

The overall trend of increase in the total number of cells in the period before workers emerged was, as a rule, linear, the average rate varying from 2·3 cells per day (C) to 1·7 cells per day (E), a difference amounting, after 20 days, to 46 and 34 cells respectively. In J and F the trend was not linear but, on the contrary, showed a continuous decline in rate of construction (Table IV).

Eggs.—In all colonies the first eggs (up to about the 10th) were highly fertile and, after an incubation period of about 5 days (see J), yielded larvae. This record was not maintained, however, and later, as has already been mentioned, it was common for a cell to be occupied by an egg for longer—up to 15 days. It is difficult to interpret this, but three possibilities would appear to exist :

(1) A prolongation of incubation for physiological or climatic reasons.

(2) Cannibalism and immediate replacement ; cannibalism caused by hunger following a reluctance to forage, again either because of a physiological maturation of the queen or for climatic reasons.

(3) Low viability of eggs (and also larvae) combined with efficient scavenging and replacement.

Examination of climatic data (given in the Appendix) provides no support for the first hypothesis and it is, in any case, perhaps unlikely that climate would cause in two different years such similar results. In support of the physiological explanation there is the observation that, in a nest with no remaining adults, eggs were seen to persist without apparent change for periods of ten days or more.

Pupae have also shown a tendency to take longer to develop the later they were formed ; here, of course, no possibility of replacement exists. Hence it is possible that retardation of embryogenesis and metamorphosis are both the consequence of a deterioration in nutrition (of the queen and larvae respectively), resulting from a diminished rate of collection of protein foods. If this were the case a trend of increase in incubation period would be expected. This occurs in J (from five to eight days), but not in E. In this latter nest a fluctuation about the period three to four days suddenly changes into (with cell 30 *et seq.*) an alternation of 5 or 7 days with 12, 13, 14 or 15 days. This is more consonant with other hypotheses.

The second of these, that cannibalism is followed by rapid replacement, has in its support the fact that removal of eggs was known to occur, for it could be detected in cases where replacement was delayed for more than a day (e.g., H cells 21, 22, 23, 24, 27), or again, in one unique case, when queen E added an egg to a cell already containing one and later removed it (E, cell 1, day 31). Very often these eggs were removed before they could be expected to hatch (e.g., H 21, 22 ; C 40, 41, 42, 43), but this may not argue in favour of cannibalism, for it is possible that a failure in development can be detected quite early by, for example, the turgidity of the egg or its odour. The fact, however, that numerous first stage larvae were destroyed early in their existence again suggests cannibalism (H 16–19; C 28, 39; E 34, 41, 46), for it occurred at a time when little or no protein food was collected (not, as far as could be seen, because of bad weather), and when the larger larvae were capable of voracious feeding if offered food directly. Consumption of brood is a regular phenomenon in ant societies, and usually falls most heavily on eggs and first instar larvae. But the curious feature of the hypothesis of cannibalism is the early replacement which is presumed to take place—a state of affairs indicative of a precarious balance between the impulses of feeding and procreation.

The third hypothesis differs principally from the second in the causes which are suggested for mortality rather than in the consequences, although it is also possible to attribute the low viability of eggs (and larvae) to malnutrition as before. This low viability could be a temporary phenomenon, ceasing when workers become active foragers, but, as none of these colonies succeeded in establishing themselves it is not even necessary to suppose this, for poor viability might be the cause of the failure. This hypothesis receives support in two ways (apart from the relevant points mentioned in the previous section). First, it is easier to credit the *immediate* replacement of non-viable eggs rather than of cannibalized eggs, and second, there is evidence that wasps do show the type of discrimination and behaviour involved. Thus one third instar larva was known to be eaten (E 9, Day 42) and, at about the same time, other old third instar larvae whose growth had been appreciably delayed were removed (not, in all cases, eaten) rather than younger larvae in the same instar.

Even though the real cause of the observed increase in incubation time has not been ascertained (and it is quite likely that all three possible explanations may be involved), there can be no doubt of its importance as a symptom of strain in the colony.

These considerations prevent the estimation of the actual rate of oviposition. In colony J the queen began with 4, 4, 2, 3, 2, 0, 2, 2, 1, 3 . . . eggs per day, and in colony E the rate appears comparable—even beyond the 29th day if internal oviposition (i.e., eggs laid in the cells from which workers have emerged and as replacements of eggs and larvae) is considered. In this nest there is an apparent lull about the 24th to 30th day. In general, oviposition is strictly limited only by space (i.e., the availability of empty cells) in the first few days (up to about Day 10 in nest J), for, after that, cells may occasionally remain empty for a short while. It is likely, however, that once a worker force is mobilized there is a return to the earlier condition of space-limited oviposition.

Larvae.—The normal period as a fixed, outward-facing larva was 3–5 days (Table V); but this was extended during the period of inanition following the first burst of activity by the queen to, in one case, 17 days (E 26). For the inward facing larvae (during this stage the major part of growth is achieved), the time was equally variable; e.g., larvae in nest J cells 1–4 took 3 days, but 6 days was the more usual time when followed by pupation. During the period of inanition some larvae were 24 days in this stage and a large number died (e.g., E 9, 11, 13, 14).

In Table VI the times from laying to pupation have been summarized. In nest C, with the best record, the brood in the first four cells took 12 or 13 days; this increased gradually to 20 or 21 days with cells 10 to 15.

Pupae.—Survival of pupae was high: in the 4 nests C, E, H and J none died. There was a noticeable tendency for the later formed individuals to take longer over metamorphosis (Table VII: nests C, E and I, queen-reared ones only), a condition rectified in nest I once the worker population had become functional. The range from 7 to 22 days could not be satisfactorily explained by weather influences, and more information on this subject will be given in a later section.

The numbers of pupae produced in nests D, F and I were ascertained accurately at various times and have been tabulated (Table VIII), together with those of the fully detailed colonies for comparison. The difference between the success of I compared with F or E is striking. The former had 9 rather than 5 or 6 pupae on Day 20; on Day 40 it had over 30 pupae as compared with 2 or 3; and by the 45th day this nest had 54 pupae.

Workers.—The first batch of workers, produced from wholly queen-reared brood, was complete by the 32nd day in I, but only nearly complete by the 43rd day in E (fig. 3 and Table VIII). In I the batch was composed of 9 workers, in E of only 6. These 9 (reduced to 6 by the 34th day as a result of foraging losses) at once finished off and pupated a group of large larvae immediately their junior, which no doubt suffered a mild period of inanition. As a result there was a second addition to the worker force, larger and quicker than the first. It seems reasonable to conclude that nest E (and also F) failed because it was unable to produce, early enough to be effective, an adequate worker force. On this basis the colony named C was, for its brief history, comparable with I—in fact it had more pupae and as many workers on the 25th day. Intraspecific competition appears to have brought disaster in this case.

The inanition phase left its mark on worker size in the two colonies where this was measured. In I (Table IX), whilst the first wholly queen-reared adults to emerge were of normal size, those next emerging, which were pupated from starved queen-reared larvae, were very small in comparison. But as the workers gradually improved the trophic condition of the colony the earlier size was once more attained. In nest F, where the wholly queen-reared workers (no others were in fact produced), were weighed on emergence, the weight was found to fall as follows: 183, 185, 177, 124, 94 and 94 milligrams. This fall in weight was not apparent in nest I, where all the queen-reared workers were large, and again points to some defect in the F colony.

By contrast, in primarily pleometrotic ants the queen-reared workers are often small (nanic)—no doubt because reliance is placed on internal reserves (except certain Ponerinae, the queens of which forage as do wasps). Exceptions to the rule amonst higher ants are certain Argentine leaf-cutter ants, *Acromyrmex* spp., which Goetsch (1939) found to produce, at first, larger workers from large eggs, and later smaller workers from small eggs.

(c) *Pellet Production.*

Although even the smallest larvae were given flesh, it was noticeable that the size of the piece taken from the masticated fly by the nursing adult was in rough proportion to the size of the larva to which it was given. The larger larvae thus produced the most conspicuous pellets.

Pellets and colony development.—The number of pellets collected each day from all seven colonies has been set out in Table X.

In all nests there was a period of pellet ejection, beginning with an increase in the population of large larvae about the 10th day and rising to a peak somewhere between the 13th and 17th day. From this time a definite, although irregular, decline set in and for several days no pellets were collected—even in the successful nest I. This decline was only relieved by worker activity, which, in I, brought the pellet-rate up to five times its maximum whilst the queen was alone; but in E, F and H, where workers were produced in small numbers comparatively late, the resurgence was not nearly as great. It is significant that throughout the period of pellet minimum there were numerous large larvae in the nests always ready to accept crushed flies—as also was the queen. The effect of this starvation phase in the history of the colonies, evidence for which emerged from a consideration of the duration of instars and the phenomenon of egg persistence, has already been mentioned.

The meteorological data for the relevant periods in both years have been carefully scrutinized and nothing has emerged to suggest that the reduction of the queen's feeding activity was caused by weather. Wasps work well in dull cool weather, even in light rain (as compared with honey-bees). It is strong wind, more than anything, which interferes with their flight. Consequently there seems no alternative but to suppose that failure to continue foraging for flies is an intrinsic property of the queen: either she is designed to work for a certain time, adequate for producing workers, or she reacts specifically, by relaxation, to a certain brood condition—for example, the formation of an agglomeration of pupae in the centre of the nest.

The fly-equivalence of pellets.—The number of flies brought in was calculated on a few occasions from the pellet production. It was of course first necessary to feed flies to larvae, singly, and collect the pellets produced.

Lucilia sericata Meigen was the fly used in all cases. It was then found that queen D carried food roughly equivalent to 35 average *Lucilia* adults on her 13th day. But this was exceptional for a queen alone, and the more usual maximum gave a figure of between 15 and 20 per day. Queen D averaged 15 per day, and H about 8 per day during their periods of greatest activity.

Pellets, worker size and pupal period.—These three factors showed correlation in the nest (F) in which they were investigated. The pellets produced by the whole nest in the two days preceding the pupation of an individual were taken as the best available index of the amount of food received immediately prior to pupation. The pupal period and the weight at emergence were recorded accurately; although only 6 individuals were available for consideration, the following correlations were obtained:

x = weight of pellets (milligrams).
y = time as pupa (days).
z = weight of adult (milligrams).

$r_{xy} = -0{\cdot}815$, P = 2–5 per cent.
$r_{xz} = +0{\cdot}936$, P = 0·1–1 ,,
$r_{yz} = -0{\cdot}919$, P = 0·1–1 ,,

No further analysis is possible. In nest E the weight of pellets and the time as a pupa were also negatively correlated ($r = -0{\cdot}884$, $P = 1$–2 per cent.), but here unfortunately the weights of the emerging workers were not recorded. In general we may conclude that the queen that feeds her progeny well not only rears large ones, but obtains them earlier than the slacker queen.

(d) *Factors Governing Successful Development.*

While the general pattern of events was similar in all colonies, there was considerable variation in the degree of success attained. Six aspects have been used for comparison :

(1) The number of cells in the nest at the 20th day.
(2) The number of envelopes started and completed.
(3) The average weight of pellets ejected per day during the period 23rd May to 5th June.
(4) The number of larvae pupated by the queen.
(5) The date of formation of the first pupa.
(6) The date of emergence of the first worker.

From this, the significant fact emerges that a queen tends to be good or bad at most of the activities which can be considered as contributing to the success of the nest. Thus for I, a successful one (and here, regrettably, data are not complete), envelope construction was more advanced than in any of the other nests (5 begun and 4 completed), a moderate number of pupae were formed (9, second only to C) and the first worker emerged early (Day 22). Nest C might well have succeeded but for interference : envelopes were well developed (4 begun, 2 completed), as also cells (45) ; a high rate of pellet ejection was maintained (9·0 mg.), the number of pupae was exceptional (15), and the first worker early (Day 22). At the other extreme, H had few envelopes (3 begun, 2 completed), few cells (29), a low rate of pellet ejection (4·5 mg.), few pupae (5)—the first not very early—and a late emergence of workers (Day 32). A full comparison of all seven queens is made in Table XI.

It seems probable that there are large constitutional variations in the amount of energy devoted by the queens to their work ; there are active and slothful queens. It is relevant to recall that, in an earlier paper (Brian and Brian, 1948), two queens were shown to differ in the amount of time spent resting. One spent significantly longer than the other coiled round the nest spindle.

The pattern of activity appears to be a compromise between two extremes : (1) *stage-periodic*, in which each batch of brood is taken to maturity before another is started, and (2) *stage-continuous*, in which a steady inflow of embryonic material is maintained and all stages of ontogeny are present at any time. Even in this latter case the size of nest (*sensu stricto*) is limited. It would be 50 cells if an oviposition rate of two eggs per day were maintained with an ontogenetic period of 25 days ; in fact, however, oviposition tended at first to exceed and later to fall below this value and a slackening of feeding activity retarded ontogeny[5]. Also, some concentration of effort on the earlier, central brood appears to have been indulged, but it is difficult to resist the reflection that an even greater stage-periodicity would have been advantageous. Ideally perhaps 15 cells might be constructed, and 15 eggs laid, resulting in the maturation of 15 large workers at the earliest possible moment, all ready to devote themselves to the nurture of a further, more numerous set of larvae.

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[5] Had it been impossible to estimate the amount of food consumed it would have been very tempting to attribute this inanition to the over-production of larvae, with consequent deleterious inter-larval competition for the limited food-carrying capacity of the queen.

3. FEEDING.

In the previous section a few aspects of flesh-feeding have been mentioned. This will now be extended, and, in addition, the role of sugary liquids in the economy of this species of wasp will be considered. Queen nests were well suited to observations on this subject, for the *sylvestris* queens became quite tame after repeated handling, and would return and feed their larvae even when the nest was held, inverted, a foot or more from its usual site.

(a) *Comparison of Species in Flesh Pre-treatment.*

A flourishing queen nest of *Vespula germanica* Fabricius was found which, surprisingly, was producing no pellets: the larvae swallowed the food given to them entire. It was found that, if given food prepared by a *sylvestris* queen, they ejected a pellet. Similarly *sylvestris* larvae, if given food prepared by a *germanica* queen, swallowed it entire, and gave no pellet! The difference was not due to the nature of the food, for adult *Lucilia sericata* were offered and treated by both species with the usual difference. Evidently the malaxation of *germanica* is more thorough, and this alone determines whether the larvae swallow the food entire or not. *V. germanica* queens spent two to three minutes instead of one minute in pre-treatment.

When account is taken of the relative efficiencies of external versus internal digestion, expulsion of waste versus ingestion of waste (and is the waste content of the foods given the same ?), and the various social effects such as increasing nursing duties at different stages of colony-development, the balance of advantage against disadvantage in the two procedures is complex. But the difference is in line with the evolutionary trends in all groups of social Hymenoptera, and supports existing evidence that *germanica* is more highly evolved than *sylvestris*.

(b) *Nature of Flesh Eaten.*

Given a period of intensive study, it might be possible to identify a great many of the insects taken as food by *sylvestris* by analysis of the larval pellets. It was noted that adult *Bibio* spp. (Diptera: Bibionidae) were an important item in the early diet. Adult Tipulidae were also taken, but later in the season, in July, small flies of Acalypterate Cyclorrapha formed the staple item. The common defoliating caterpillars were not collected, although they might occasionally be accepted when offered to a queen on the nest; even so, she had great difficulty in malaxating their tough (rather than brittle) cuticles, and the larvae also took much longer to dispose of these. One queen was offered a number of other insects: all adult Diptera available were accepted; Aphididae were accepted, but spiders, beetles and ants were refused. On one occasion a queen that had repeatedly accepted and treated flies in the usual way applied one to an envelope as though it were pulp.

(c) *Exchange of Fluid between Adults and Larvae.*

When the queen returned with neither pulp nor flesh she visited each larva, putting her tongue to their mouths, and a drop of fluid passed between them. This was usually followed, a few moments later, by another action: she went to some of the larvae (not necessarily the same ones), vigorously pinched their prothorax with her mandibles, and again a drop of fluid passed between them.

This act took place at other times as well. When the queen was given syrup stained with fuchsin, she drank it and distributed it a few seconds later to the larvae. On pinching them she obtained a colourless droplet. This could also be done " by hand," that is, without the mediation of the queen, with the same result—the larva drank the coloured syrup and gave up colourless salivary secretion.

The fluid given by the queen (and later by the workers also) was, almost certainly, either " honey-dew," that is, the surplus juices exuded from the anus of plant-sucking Homoptera, or nectar from open flowers. The principal sources of honey-dew were oak (*Quercus robur* L.), and hawthorn (*Crataegus* sp.). Nectar was obtained from the flowers of raspberry and later blackberry (*Rubus* sp.), plants of which had often many wasps visiting them. They were also seen collecting nectar from the flowers of *Rhododendron* and hawthorn, although on the latter plant they clearly found the Homoptera more attractive.

(d) *The Time Devoted to Fluid Foraging.*

Fluid-collection forms an important part of *sylvestris* activity. More foraging trips are for fluid than for the other two substances, and the average duration of a trip for fluid is longer. Hourly samplings were made of the work of four queens (C, F, I and J) and all the workers of nest I. The queens together, in 7 hours, made 25 trips for fluid, 12 for pulp, and 8 for flesh; the workers, in 23 sample hours, gave figures of 232, 173 and 140 respectively. The average times taken for a load were (queens) 8·1, 5·6 and 3·1 minutes, and (workers) 10·9, 8·5 and 6·1 minutes respectively (Table XII). Thus more loads of fluid were collected than of any other material, and both queens and workers took longer to collect fluid than the other substances. For some reason, also, the workers were, in all cases, slower at a particular task than the queen. When these observations are combined it is found that, of the total time spent foraging for food (fluid and flesh), the queens spent 88 per cent. and the workers 72 per cent gathering fluid.

(e) *The Salivary Secretion of the Larva.*

Quantity.—A very variable amount of saliva was obtainable from a larva *in situ*—sometimes nothing, sometimes as much as 10 cubic millimetres at a time. It was found, by hand culturing, that the larvae that gave copious quantities of saliva were the ones that had earlier received a good deal of fluid. But there was a time-lag in availability, and, even then, the rate of production was limited. Thus, a larva weighing 110 mg. after complete removal of saliva by repeated stimulation and collection, was kept in an artificial cell and fed on 20 per cent. sucrose solution. After 30 minutes its weight had risen to 170 mg., an increase of 55 per cent. It was not until a further 30 minutes had elapsed (one hour from the time feeding was started) that any saliva could be obtained, but then it came easily. Nevertheless, it was only after four hours of repeated " draining " that it returned to its original weight. The resemblance of this process to water excretion in other insects is striking.

The effect of not removing saliva from larvae was then investigated. A suitable nest was taken, the adults removed, and the large larvae divided into two groups. Both were fed mashed fly and 20 per cent. sucrose at frequent intervals, but one group was desalivated regularly, and the other not at all. After 2 days the first group were quite normal in appearance and behaviour, but the second group were conspicuously distended and salivated copiously immediately their mouths were touched with food, thus interfering with the progress of the experiment. On one occasion only did a larva expel fluid spontaneously without apparent stimulation—and the next day it was dead! Any drop of liquid, even water or sodium carbonate solution, left on the mouth was swallowed. It seems justifiable to conclude that larvae only salivate, even when turgid, in response either to food, or to being "pinched" by a nurse. This is of great importance, for if dribbling were a common practice it might easily lead to a loss of coherence in the nest fabric through wetting. The fluid so gathered by nurses is swallowed, and presumably passes through their gut. They excrete a watery urine, pale yellow in colour, and are careful to come to the nest entrance and shoot it well away—in fact this is the only occasion on which the queen is seen after she has stopped foraging. Hence we may tentatively suggest that, as a result of obtaining carbohydrate in dilute solution, the larvae need to excrete excess water and this is done, not by the Malphigian tubules, which, as in many other Hymenoptera, do not have access to the outside since the anus is blocked, but by the salivary glands[6]. Finally, ejection of saliva is confined to those times when the workers are present to remove it.

Character.—It has been reported that sugar is present in larval saliva. A number of micro-chemical tests confirmed this and indicated that it was probably glucose. Fructose and sucrose were not detected. A strongly proteolytic enzyme was present and, no doubt, as a consequence protein reactions were given by the saliva. No urea or uric acid could be detected, but ammonium was undoubtedly present; it is, however, unlikely that this is a significant method of nitrogen excretion. Larvae store uric acid in the lumen of the Malphigian tubules, and in large individuals it occasionally escapes through a minute pore in the anal septum[7].

The hydrogen ion concentration of the saliva showed wide variation. From a normal value of about pH 6 it would rise, if a larva was repeatedly desalivated, until the last withdrawals were alkaline with a value of about pH 8. Saliva, pH 7 on secretion, changed in one day when stored in a tube, to pH 4. It is reasonable to conclude that on secretion into the salivary reservoir the saliva is alkaline, but that on standing it changes much as it does outside the body.

From the foregoing it is clear that saliva cannot be solely a means of water excretion; for it certainly has a digestive function, and may account for a little loss of nitrogen. The glucose might be an unavoidable "leak," or perhaps a co-enzyme, but the possibility cannot be dismissed that it may play some part in social function. Its quantity was not investigated chemically as the complications caused by the amount of protein made this beyond the capacity of the investigators, but a number of biological tests, perhaps not less important, were performed.

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[6] Water excretion through the anus would, of course, damage the nest fabric in exactly the same way as uncontrolled salivary excretion.

[7] In ant larvae (at least those of the genera *Myrmica*, *Formica* and *Lasius*) the Malphigian tubules have access to the outside through the hind gut and anus which is open, and the watery urine is carried away by workers; in *Bombus* this is the case only in the last larval instar, and in *Apis* not until prepupation.

(f) *The Behaviour of Adults towards Larval Saliva.*

In the first experiments a queen without workers was offered a series of fluids in a pipette. The fluids used were 5 per cent. sucrose, larval saliva, and water, and they were offered either in pairs or successively. The sucrose concentration was chosen to represent an unusually dilute nectar. It was always accepted eagerly in preference to the other two liquids. Only on one occasion, after a queen had been given a great number of flies, were water and larval saliva accepted, and even then it was quite clear that the sugary solution was preferred. These results were confirmed later in the season with workers.

This type of approach was extended to field conditions. Workers of *V. rufa* were conditioned to a source of sucrose; this was then replaced by a pair of fluids absorbed in cotton-wool and placed about a centimetre apart. The workers preferred 20 per cent. sucrose to 10 per cent. sucrose, and 10 per cent. sucrose to 10 per cent. glucose. They also preferred 20 per cent. glucose to saliva, but failed to discriminate between 10 per cent. glucose and saliva. They easily lost interest in these last fluids and, if only slightly disturbed, went away.

These results point to the conclusion that larval saliva is intrinsically unattractive and, although containing glucose, this is present in such small quantities (perhaps 10 per cent. or less) as to be of negligible use as an attractant or stimulant. It is interesting to contrast these results with statements in the literature that workers " eagerly " or " greedily " induce larval salivation. There is no doubt that the pinching action is vigorous, if not violent, but in view of these results it seems easier to regard it as a sign of zealous attention to larval and nest welfare rather than a selfish greed. In fact, there appears to be no evidence to support the hypothesis that the glucose present serves some social purpose.

(g) *Experimental Modification of Larval Diet.*

By rearing larvae by hand, it was possible to study the effects of sugar deprivation. Moderate-sized larvae in nests which had been accidentally rendered queenless were used and the nests were kept warm under the quilt of a honey-bee colony—the best available controlled source of heat in the field. Larvae were divided into two groups: a control, fed three times a day on crushed fly and six times a day on 50 per cent. sucrose solution; and an experimental set, fed three times a day on crushed fly, and six times a day on water. The control larvae remained active throughout the experiment, secreted saliva —containing glucose—copiously, and showed especially vigorous mandibular movements when given flies and even sugar solution. They formed a depression ventrally between the head and thorax in which the droplet of liquid was held. The larvae deprived of sugar were at first quite active and masticated crushed flies, but, although they swallowed water, they made no simultaneous mandibular movements nor did they form the ventral depression or receptacle. After 24 hours a slackening in activity was apparent; after 48 hours they were clearly moribund and unable to feed. The smaller larvae were slightly more resistant, perhaps because of their lower energy requirements for although wasp larvae remain in a cell, their digestive processes must require considerable fuelling.

From these results we may conclude that the large proportion of work devoted to the collection and administration of sugary fluids to larvae is necessary for their well-being and is not, as might at first seem possible, a storage device. The idea sometimes put forward that the sugar in saliva is derived from the protein foods administered and is superfluous to larval requirements, is totally erroneous.

(h) *Fluid as a Larval Food in Wasps.*

Considerable confusion exists about the prevalence of fluid as a larval food in wasps and whether, when given, it is the juice extracted from prey, or plant juice, or a mixture of both. Réaumur (1742), writing of social wasps, says:

> ". . . j'en ai observé qui ne donnaient qu'une goutte de liqueur à sucer à des vers déjà gros et j'en ai observé qui donnaient à des vers encore plus gros les aliments solides."

Siebold (1871) recorded *Polistes* females introducing their heads into cells when without pellets and disgorging fluids to larvae. Roubaud (1916 : 123) comments:

> "Il est probable que la goutte de liqueur dont parle Réaumur représente en réalité la sécretion salivaire de la larve humée par le guêpe nourricière."

But it seems likely that Roubaud was wrong, for he later says of *Belonogaster* spp. (1916 : 126):

> ". . . il y a une disproportion flagrante entre la quantité de nourriture distribuée aux larves par les femelles et celle du liquide salivaire que celles-ci reçoivent en retour. Il y a alors exploitation réelle des larves par les nourricières."

This, if true, necessarily implies that the helpless larvae are at some time given fluid by the workers. Duncan (1939 : 115) retains an open mind, and is prepared to believe that sugary plant juices may be fed to larvae alone or mixed with animal juices. In *Vespula sylvestris*, as has been shown, much time and energy is spent on the collection and administration of fluid of plant origin (nectar and honeydew) to the larvae, for whom it is indispensable.

It would be interesting to know how and at what stage in evolution the dual feeding habit developed. In the genus *Synagris* (Eumenidae), studied by Roubaud (1908, 1910*a*, 1916), dual feeding appears to have followed progressive provisioning very closely. Two species, *S. spiniventris* Illiger (called by Roubaud, *S. calida* L.) and *S. calida* L. (called by Roubaud *S. sicheliana* Saussure) mass-provisioned with caterpillars when these were abundant but, in times when food was scarce, the egg often hatched before adequate food had been collected. This incipient progressive provisioning was only rarely accompanied by any malaxation of the prey, but *S. calida* occasionally lightly malaxated caterpillars in the head region[8]. A third species, *S. cornuta* L., not only regularly practised progressive provisioning, but malaxated and extracted the juices of the caterpillars. It fed a paste to its larvae. Roubaud then comments on the fact that the larvae salivate copiously when this relatively dry food is offered them, and remarks how desirable such a saliva is for dealing with it! Evidently, as with *Belonogaster* and other higher wasps, the larva was being given fluids, possibly partly of plant origin, at other times.

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[8] Malaxation must be the prelude to juice extraction, although in itself it does not necessarily involve it.

The change within the genus *Synagris*, as it exists to-day, is thus quite sudden and malaxation and dejuicing appear to be correlated with the change from mass to progressive provisioning[9]. Perhaps *Zethus cyanopterus* (Williams, F. X., *in* Wheeler, 1923), which feeds its larvae "from day to day on small caterpillars which have been partly eaten," lies between the two *Synagris* species.

This relation between the water content of the diet and water excretion in social Hymenoptera is of much interest. Presumably very little or no excretion of water is necessary with mass-provisioned larvae, and water elimination is associated with those forms of progressive provisioning that involve dual feeding. In Apidae (also showing dual feeding) the concentration of nectar, that is its conversion into honey, may reduce or obviate the necessity for water elimination in their larvae, and perhaps account for the absence of "trophallactic larval salivation."

(i) *Oecotrophobiosis and Trophallaxis.*

The results of this section may be summarized as follows :

(1) Larvae do secrete sugar, probably glucose, but in such dilute concentrations that the solution in itself is not attractive to adults.

(2) A considerable amount of time is spent collecting sugary fluids which are essential for larval life.

(3) Excess water is voided, not by the usual channels which are closed, but in the salivary secretion, the flow of which is, as a result, related to the amount of fluid in the diet.

(4) Extrusion of the fluid is controlled and takes place only when food is given, or at a signal from the nursing worker. As a result collection of the fluid is possible, with later deposition outside the nest.

(5) The glucose appears to have no social significance. It may be a vestige of an earlier stage in social evolution, or, perhaps, a co-enzyme, or merely an unavoidable leak.

Before examining the bearing of these results on the oecotrophobiosis or trophallaxis theories it is advisable briefly to consider the history and meaning of the ideas involved, for cases of uncritical and unwarranted usage are widespread in modern literature on social insects.

Roubaud (1910*b*), after studying three species of *Belonogaster* Saussure, said that the culture of the young,

> ". . . si frappant chez les Guêpes sociales, a dû tirer ses origines mêmes de la gourmandise de femelles."

He described the adults as feeding themselves on plant juices and their brood on various small animals, principally caterpillars. After removal of the intestine these were malaxated, and after some of their blood had been swallowed, given to the larvae as a paste. The nursing workers then went to each larva and provoked the secretion of a " liquide incolore et limpide," which they eagerly removed. Thus the feeding of *Belonogaster* spp. closely resembles that of *Vespula sylvestris*, except that Roubaud did not mention any passage of liquids *to* the larvae. His refusal to accept the ideas of the earlier naturalists (notably Réaumur and Siebold) sprang, no doubt, from a desire to champion the oecotrophobiosis theory ; according to this theory it is " natural " for wasps to breed and closely tend larvae when such delicious fluids can be obtained from them— and, we might add, clearly unnatural to give them a lot of sweet fluids at the same time ! Roubaud extended his ideas to termites and ants (in the form of brood-licking), and thought that further knowledge of bees might enable its application there also[10].

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[9] This, however, is by no means always the case with Vespoidea and Sphecoidea, for malaxation and mass-provisioning and non-malaxation and progressive-provisioning are often associated.

Wheeler (1918), after ironing out the grosser inconsistencies of Roubaud's theory, gave numerous illustrations in ants. Some were like wasps, but others exuded materials through the skin, often from well-developed exudate organs. He preferred the word " trophallaxis," partly because he could not accept the suggestion that adults exploited larvae, and partly because he wished to distinguish this " mutualistic " condition from such relationships as that between ants and their aphids, which " so far as nutrition is concerned, is one-sided, since the ants exploit the aphids, etc., and may defend and even transport them, but do not feed them."

Later (1928), Wheeler extended trophallaxis to include—

> ". . . its role as a stimulus, or excitation of the chemoreceptors. Obviously this latter role is of the greatest significance in social organisms."

Thus the concept began to move away from its initially *cohesive* form towards a *kinetic* form ; it no longer described a means of social cohesion, but a method of social activation. This evolution was completed recently by Schnierla (1944 : 178), who, writing of *Eciton*, stated :

> " It is a common observation that stimulation from passing workers may arouse quiescent larvae to squirming activity, or that chance stimulation from larvae may bestir workers. It is manifest that the larvae thus in a number of ways arouse the adults to increased activity, in the mutual stimulative relationship between adults and brood which Wheeler (1928) has termed 'trophallaxis'."

The activity of the larvae causes the workers to forage further and more energetically, and has as a consequence a daily change of camp. The brood condition thus governs the alternation between static and nomadic phases.

The situation in *Eciton* then, where kinesis is mutual, can be interpreted on the cohesion basis as follows : The larvae obtain food, and, in exchange, the workers obtain self-fulfilment, involving no doubt much chemostimulation. But this has brought trophallaxis to complete equivalence with " maternal instinct," which it was originally introduced to replace.

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[10] It is curious that the method which ants adopt for disposing of larval urine has never, so far as we are aware, received the attentions of trophallaxis exponents. This fluid (at any rate in *Myrmica rubra* L.) is expelled in response to a slight mechanical stimulus on the ventral abdomen, and is then either swallowed, or carried away in the mandibles of the nurse and put on the rubbish heap. There is here every indication of resemblance to *V. sylvestris*, except that the ant larvae can without disadvantage use their Malphigian tubules in the ordinary insectan fashion. *Myrmica* also practice dual feeding.

Nevertheless it is possible that the ideas of Roubaud (excepting exploitation) and the earlier ideas of Wheeler may still be so useful as to warrant a special name. In 1918, before he had been goaded into extending his meaning, the latter author wrote:

> " But even if it should be found, on further investigation, that there is no indication of reciprocal feeding between the larval and adult Bombinae and Apinae, we might still contend that these highly specialized insects had in their evolution passed far beyond the stages represented by the termites, ants and social wasps."

An evolving behaviour pattern associated with reproduction may develop with the assistance of, or possibly incorporate some elements of, pre-existing behaviour patterns associated with nutrition.

Licking of offspring, as in ants or mammals, which has hygienic advantages, may be brought about by incorporating a substance in the coating which elicits a trophic response. But, for the first step, whether the method be trophallactic or instinctive, a change in one of the participants is necessary —in the wasp for example, where a need for the larva to excrete water arises, either it must introduce sugar into its saliva (the trophallactic method), or the adult must develop a new pattern of behaviour (the instinctive method). Which is more easily accomplished ?

In *Vespula sylvestris* feeding and nursing behaviour has evidently passed beyond a trophallactic stage, if such ever existed, but investigation of the sugar concentration in the saliva of more primitive wasp larvae, significantly interesting to the nurses, might provide evidence of a trophallactic stage in wasp evolution[11].

4. FORAGING.

The successful colony (I) was conveniently situated for observation. Workers were marked with cellulose paints of various colours, and their foraging studied at the nest entrance in one-hour periods of observation at different times of day from 11th to 22nd June inclusive (days 32–43).

Compared with other social Hymenoptera of which we have knowledge, the workers take an active part in the affairs of the colony very soon after emergence. After a few hours, during which they usually stand on the comb with their head in a cell, they may assist in the mastication of flies brought in by others. They forage after only a few days; of 15 workers studied, 10 began to forage on the day following emergence, and 5 two days after emergence. This compares with about 20 days for the honey-bee (*Apis mellifera* L.), 5 or more days for certain species of *Bombus* and certainly at least several weeks for many ants (e.g. of the genus *Myrmica* Latreille). (The changes which took place in the worker force immediately preceding the period of observation are summarized in Table XIII.)

Out of a total of nine workers, three vanished, never returning from foraging trips. These, and the six which did most of the foraging during the period, emerged from the first batch of pupae. The second batch, worker finished, began yielding workers on the 19th June (Day 40). The foraging of the queen slackened as soon as, or only slightly after, the workers' began, although it is quite possible that she had reduced her outdoor activity earlier than this; she was not seen to go out after the 33rd day. It is probable that this change is related in some way to the presence of foraging workers, for one queen, who produced only three workers which she later lost, frequently left the nest, flying heavily, as late as the 50th day.

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[11] The concentration in *V. sylvestris* is not high enough to cause a sweet taste to man, yet Du Buysson (1903) and Janet (1903) detected sweetness in the saliva of (unspecified) *Polistes* spp. and *Vespa* spp.

The behaviour of foragers in the field differed characteristically with different activities. Wasps seeking flies moved rapidly and with great agility, and were very sensitive to human presence. They hunted in places where plants and pulp sources were absent, such as stone walls, as well as along hedgerows and amongst flowers. Many small flies, principally of the Acalypterate families of the Cyclorrapha, were caught whilst feeding on nectar in open flowers of various Umbelliferae[12]. The wasps approach rapidly, pounce, and move off. Fluid-gathering wasps moved much more slowly, examining the groups of Homoptera on or under the leaves of plants, or passing from flower to flower in the manner of honey bees. Pulp was gathered from dead but not rotten wood (which *V. vulgaris* is reputed to favour).

Even in the week preceding the summer solstice the wasps worked from sunrise to sunset (roughly), making a day of nearly 18 hours, but for about half to one hour before sunset and after sunrise they flew heavily and often failed to land on the nest. It is not surprising that they never brought in flies on these occasions.

(a) *Materials Collected.*

545 loads were carried into the nest, of which 42 per cent. were fluid, 32 per cent. pulp, and 26 per cent. flesh. The occurence of mixed loads was unlikely for various reasons. Thus, apart from the characteristic "mannerisms" just described, there are the following arguments: that flesh-gathering had a characteristic journey-time and a characteristic time of day, and that fluid-gatherers returned with distended abdomens, flying heavily.

The loads collected during 23 sample hours of observation have been subclassified according to material-type and period of collection: up to 8.00 hrs., 8.00 to 17.00 hrs., and after 17.00 hrs. (G.M.T.). Sunrise at this time was 3.30 hrs. and sunset at 21.05 hrs. (G.M.T.). In the first period (4 sample-hours), 35 loads of fluid, 19 of flesh, and 16 of pulp were collected; in the middle period (13 sample-hours) the corresponding figures were 129, 45 and 143; in the final period (of 6 sample-hours) 68, 76 and 14 (Table XIV). The distribution is not homogeneous for relative load-type frequency in each period (by χ^2, $P<0{\cdot}1$ per cent.). Flesh was collected more in the evening, when it ranked as high as fluid, and pulp was low. Conversely, pulp ranked high, higher than fluid, in the mid-day period when flesh was low. But in the early morning fluid loads were twice as frequent as either of the other two. In fact, flesh and pulp were roughly interchangeable in the total activity, and, if grouped together and compared with fluid collection (using χ^2 test), gave no indication that any changes other than chance variations of work distribution (between the two artificial groupings) took place throughout the day. In the three periods into which the day was divided, fluid loads comprised 51, 40, and 45 per cent. respectively of all loads. The rate of gathering fluids advanced slightly from 8·8 loads per hour in the morning, through 9·9 to 11·3 in the evening. The rates for flesh were, in corresponding periods : 4·8, 3·5 and 12·7 per hour, and for pulp, 4·0 ,11·0 and 2·3 per hour.

---

[12] *Vespula vulgaris* showed interesting differences. It hunted for Capsid bugs at a lower level in the herb layer, and its movements were slower and easier to observe.

The heavier flesh intake in the evening was confirmed by the pellet-ejection data (Table XV). On each of 9 days the numbers of pellets collected in the evening were more than those collected in any of the three equivalent periods in the earlier part of the day. The totals collected in the periods 8–11, 11–14, 14–17, and 17–20 hours G.M.T. were 389, 347, 493 and 876 (sunrise, 3.30 hrs., sunset, 21.05 hrs. G.M.T.). Even more pellets (939) were collected during the night, that is from 20.00 hrs. to 8.00 hrs. G.M.T., but as this includes 5½ hours during which the sun was above the horizon (1 hour in the evening and 4½ hours in the morning), the numbers have to be correspondingly reduced.

These diurnal fluctuations in the activity of the colony were the result of consistent trends shown by a majority of the workers ; they did not result from changes in the individuals composing the working group, for all individuals foraged throughout the day. In spite of a general similarity in behaviour trend interesting exceptional individuals existed and will be discussed later.

(b) *Times Taken.*

Altogether 359 journeys were timed (Table XVI). In spite of considerable variation there is, in all cases, a modality in the frequency distributions which, after appropriate transformation, were found to differ significantly (F test : $P < 1$ per cent.). The average times taken for flesh, pulp and fluid were respectively 6·1, 8·5, and 10·9 minutes. That fluid collection took longest is not surprising. Pulp collection requires a short spell of hard work usually at a repeatedly visited site. It is curious that fly-catching should be so rapid, and we have developed the hypothesis that the wasps, if they fail to find a fly early, go on and gather fluid, for it is difficult to conceive that flies can always be so easily collected. In support of this hypothesis is the fact that, although the numbers of flies collected varies diurnally, the times taken to collect them do not show any detectable differences. If flies were persistently hunted it would be expected that, when fewer were brought in, they would take longer to catch and *vice versa* when large numbers were brought in. This subject will again be referred to when worker individuality is discussed.

The time spent in the nest between trips averaged $4{\cdot}5 \pm 0{\cdot}19$ minutes (standard deviation 3·61 minutes) for the 358 occasions recorded. This period showed no correlation with the type of load that preceded it—a surprising fact, because the nest activities following different loads were naturally different. Thus, whilst a worker applied the whole of the pulp collected herself, she was usually assisted in the distribution of flesh or fluid by the queen or other workers. The low variability of this time is also remarkable, and suggests the possibility that an important constitutional characteristic is involved. (The significant difference in mean resting time between two queens referred to in an earlier paper is again relevant.)

Before passing to the next section it is worth commenting on the fact that the workers have the same pulping routine as the queen. Before application of the pulp to an envelope they invariably enter the nest for one or two seconds. This rule has only been broken by one individual, and then only in its first few days of foraging.

(c) *Ontogenetic Changes.*

By the last day of observations (regrettably terminated by circumstances beyond our control), 9 young workers were helping the earlier 6 in foraging. They gathered all three materials, but showed a definitely higher proportion of pulp in the total—59 per cent. of loads were pulp as compared with 15 per cent. for the older workers. There is no doubt of the significance of these results (Table XVII: by χ^2 $P < 0{\cdot}1$ per cent.). The older workers gathered much more fluid.

Consideration of the ageing effect in the first six workers is somewhat hampered. Of only one (No. 6) was the exact age known; two of the others (unfortunately unidentifiable) were known to be two days old on the day when observations began. These three wasps were the youngest, and the records showed that for each of three individuals a trend of diminution in pulp collection was manifest (Table XVIII). Taking the reasonable liberty of considering these three together (for separately the figures are not adequate for statistical test) and comparing the first three days record with the remaining 8 or 9 as the case may be, a highly significant result may be obtained (χ^2, $P < 0{\cdot}1$ per cent.). The combined figures are, in terms of loads of pulp, flesh and fluid, in the first three days of foraging, 43 : 5 : 18, and in the next 8 or 9 days, 26 : 28 : 40. The initial predominance of pulp collection gave way to a predominance of fluid collection.

This ontogenetic trend in the foraging behaviour of workers is of course paralleled by queen behaviour, for pulp collection for envelopes and cells figures much more in queen activity during the first few days than later[13].

It has already been mentioned that workers whilst in the brief pre-foraging stage will masticate flies. They also spend a good deal of time breaking down internal envelopes and carrying the pulp outside for the extension of newer ones. These activities are not, however, peculiar to them, and older workers will do the same.

(d) *Individuality in Worker Foraging.*

The actual load sequence.—The following is the load sequence observed in a series of intermittent hour-samples for worker No. 2 (details for all the workers are given in Table XIX):

> PPP : PPPP : PNPPPP : PPPP : PPPP : fpnp : NNPN : ppn : PNPN : FNNPN : FPNFP : *nnn* : FFFPF : FPNPP : *nnn* : *nnn* : NNFN : nfffffff : *nff* : nnfff : *ffffff* : NNPN : *ffnfffn*.
>
> (n = fluid, p = pulp, f = flesh; mid-day records in capitals, records prior to 8.00 hrs. G.M.T. in normal print, and records after 19.00 hrs. G.M.T. in italics; each hourly sample is separated by colons.)

The trend from pulp towards fluid and flesh collection in workers 2, 4 and 6 is discernible as long as central-day data only are examined. This trend, and the diurnal variation, when taken with the fact that only a small number of loads were customarily gathered per hour (in other words, one hour is too short a sampling period for the purpose), prevent consideration of the randomness or otherwise of the activity distributions. Little more can be said than that sometimes all three activities were well mixed ; at other times sequences of a single activity occurred. Continuous repetition of the same type of activity may lead to its internal extinction and be followed by another type (recall for example the queen that applied fly to an envelope) and, in this way, a fair mixture of activities may be produced.

---

[13] It is sometimes supposed that honey-bees show an ontogenetic trend in their *foraging* behaviour from pollen gathering to pollen and nectar gathering, but we know of no published evidence for this. Comb construction is undertaken by younger bees, but before they have started foraging.

Differences in materials collected.—The individuals differed in the way in which their work was distributed between the three activities (fig. 4 and Table XX : in the test for homogeneity, the value of χ^2 was $< 0{\cdot}1$ per cent. P).

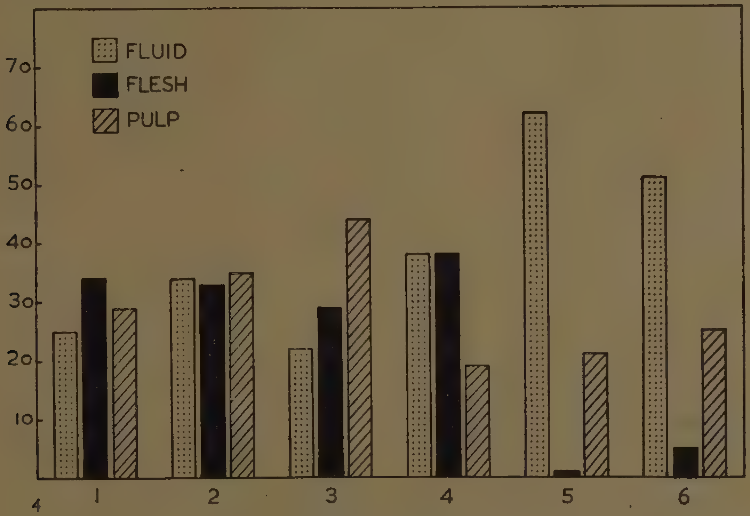

Fig. 4.—The number of loads (ordinate) of fluid, flesh and pulp, collected by six workers numbered 1 to 6.

Worker No. 3 stands out as a collector of pulp. Nos. 5 and 6 gathered very few flies and, curiously, the latter gathered all five in the last hour of observation ! These two compensated by a greater collection of fluid—perhaps they were unskilled at fly-catching so that they repeatedly went on to gather fluid (see earlier hypothesis), perhaps they worked an area poor in easily captured flies but rich in nectar or honeydew, or perhaps they were constitutionally different from the other workers (to mention three of the many possibilities). In spite of these variations the total activity shows surprisingly little variation from worker to worker—ranging from 84 to 102 in the total of 23 hours.

These differences in behaviour were not associated with differences in size, as all the six workers were much the same in this respect. Even the comparatively small workers that emerged later were seen to collect all three substances. In the Bumble-bee, *Bombus agrorum* F., the smaller workers when they forage only collect nectar, whereas the larger ones, which forage regularly, collect pollen as well (Brian, A. D., *unpublished*). Such caste dimorphism with associated labour-differentiation has been carried even further in many ants (Formicidae). Perhaps more extensive studies of the foraging of individual wasps may establish a difference between types collecting sugar and protein and types collecting very little protein (as in *Bombus agrorum*), although it is doubtful if any associated dimorphism will emerge.

Whilst pulp collection was predominantly a central-day activity for all workers, they differed in the way in which their flesh and fluid-gathering journeys were distributed through the day (Table XXI: in the χ^2 test, after grouping early with late records, the following probabilities of homogeneity were obtained: pulp 70–80 per cent., fluid $< 0\cdot1$ per cent., flesh $< 0\cdot1$ per cent.).

Worker No. 1 was unusual in gathering very little fluid in the morning and evening; in the latter she collected flesh instead. Worker No. 6 collected more fluid than usual in the evening; she was one of the two that collected very few flies at any time. Worker No. 4 differed in that she collected more flesh in the central than in the late period of the day; she also gathered more flesh as a whole than the other workers. No explanation of these curious idiosyncrasies can be offered. If they are not genetic they may arise through differences in the areas foraged by different workers, if specific areas are habitually resorted to. Some may provide easily accessible flies, others abundant fluids, and so on. If these places had different aspects, the times of day at which they yielded wasp-desirable products might vary accordingly.

Timing of journeys.—All workers divided their time more or less equally between field-work and house-work. The times spent in the nest between journeys gave no detectable differences when analysed either between individuals (F test: $P > 20$ per cent.), or, as mentioned earlier, following different activities (F test: $P > 20$ per cent.). Of the three outdoor activities, the foraging time for two, flesh and pulp showed differences between individuals (F test; gathering flesh, $P < 1\cdot0$ per cent.: gathering pulp, $P < 0\cdot1$ per cent.), whilst fluid collection showed no detectable differences between individuals ($P > 20$ per cent.). These results are summarized in Table XXII.

As far as the collection of flesh was concerned, worker No. 1 was twice as quick as worker No. 2—an unusually slow one. This latter individual was also slow at collecting fluid, but quite quick when it came to pulp. Worker No. 1 was quick at fluid collection, but by no means outstanding at pulp, and in general there is no indication of an association between speeds at the different activities; that is, there are not generally slow or generally quick workers, but some excel at one, others at another activity. However, the average times for collecting fluids and flies might correlate if more data were available. If so, this would provide more evidence for the hypothesis suggested earlier, that the two are sought in one journey, and flies are taken, if at all, only in the first few minutes. Pulp, the times for which appear independent, is in all probability gathered elsewhere. Wasps, whilst actually gathering pulp, refused proffered flies, and only become interested in sugar after much persuasion and interference.

The cause of the differences in the times taken to collect pulp is again a matter for speculation. Some workers might go to a more distant source than others; some sources might be more easily masticated than others. We do know that the size of load varied (visibly), a factor which was estimated by measuring the length of the strip applied to an envelope on various occasions. Worker No. 4, a quick collector, applied the longest strip (an average length of 1·5 inches), whilst worker No. 3, the slowest collector, applied the shortest strip (average length 0·4 inches). This certainly suggests that No. 4 was working an easier source than No. 3. But one complication must be mentioned: worker No. 3 gathered more loads than any of the others. Thus it might have collected as much pulp as No. 4, but in a different way.

(e) *Organization of Work.*

It has thus been established that the colony as a whole brought in fluids regularly throughout the day, but tended to collect more flies in the evening and more pulp in the middle-day. This represented the combined activity of all the workers as far as pulp collection, and of the majority of the workers as far as flesh collection was concerned. All the workers engaged all the time in all three foraging activities (except that two collected few or no flies).

Nevertheless, considerable individuality existed involving the proportions of the three materials collected, differences in the diurnal variation of this proportion, and differences in the times taken to collect the various substances (pulp and flesh). The ontogenetic trend from greater pulp collection towards greater fluid collection further complicated the mass results. In fact it is interesting to enumerate the few points on which significant differences could not be detected. These were the time spent resting between loads irrespective of what comprised the load, the collection of more pulp in the middle-day, the time taken to collect fluid, and the general rate and degree of foraging activity.

This last factor and the ontogenetic trend previously mentioned suggest that foraging behaviour is largely innate. Some of the individual differences support this view, whilst others seem more plausibly explained either as resulting from external accessibility variations and, perhaps, habitual foraging areas, or variations in larval demand. Many of these questions may respond to further observation and experiment in the field, and especially to experimental alterations in the trophic condition of the colony.

5. SUMMARY.

1. The nest development and brood sequences in a number of nests of *Vespula sylvestris* Scopoli have been described. An estimate of the protein food consumed was obtained by collecting the pellets of unswallowed material ejected by the larvae. It was found that, in all cases, an initial burst of activity by the queen, which led to the formation of a few pupae, gave way to a decline during which numerous larvae were starved until workers appeared. It is concluded that development is intermediate between the stage-periodic and the stage-continuous types and that there are good reasons for supposing that maximum efficiency is not obtained in this early period. The queens differ in their general degree of activity, a factor which rather than their method of work apparently governed their chances of success.

2. An investigation of the "trophallactic" reaction between larvae and adults produced the following results: Glucose is present in larval saliva but

in quantities so small as to give it no special attractive property ; a great deal of time is devoted to collecting sugary fluids and to feeding these to the larvae which cannot survive without them ; excess water is excreted from the salivary glands, but only at a signal from one of the nurses, an arrangement effectively preventing nest-wetting and consequent loss of stability in the fabric. It is suggested that in *V. sylvestris* the trophallactic stage in the evolution of social cohesion, if it ever existed, has been superseded.

3. A study of the foraging of workers showed that flesh tended to be collected more in the evening (and possibly in the morning), that pulp was predominant in the central part of the day, but that fluid was gathered steadily throughout. It was found that, in general, the collection of fluid required most, the collection of flesh least, of the time spent foraging. Workers collected all three types of load when they began work on their first or second day after emergence, but in the first three days pulp predominated, later giving way to fluid. These general properties of the colony were achieved in spite of some considerable worker idiosyncrasy with which no morphological differences could be associated.

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THE MORPHOLOGY OF THE HEAD OF LARVAL HYMENOPTERA WITH SPECIAL REFERENCE TO THE HEAD OF THE ICHNEUMONOIDEA, INCLUDING A CLASSIFICATION OF THE FINAL INSTAR LARVAE OF THE BRACONIDAE.

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(*Hope Department of Entomology, University of Oxford.*)

Manuscript received 3rd January, 1951.

(Read 7th November, 1951.)

With 34 Text-figures.

General Introduction.

This study has two aims. The first is to investigate the morphology of the head in the larvae of Ichneumonoid Hymenoptera. The second is to use this knowledge of larval morphology in constructing a key for the identification of final instar Braconid larvae. It was thought convenient to divide the study into two parts in accordance with these aims. The economic entomologist using the taxonomic section will rarely wish to work through the details of the morphology of the head.

PART 1.—THE MORPHOLOGY OF THE HEAD OF LARVAL HYMENOPTERA, WITH SPECIAL REFERENCE TO THE HEAD OF THE ICHNEUMONOIDEA.

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1. INTRODUCTION

This study is primarily an attempt to analyse the structure of the head of Ichneumonid larvae. The aim throughout has been to homologise[1] the head structures of Hymenopterous larvae with those of [illegible] insects. A [illegible] study of [illegible] [illegible] [illegible] was therefore made as a preliminary to this work.

In order that structural characters within the Hymenoptera might be correctly assessed, it was necessary to examine the heads of groups other than the Ichneumonoidea. Examples of the Symphyta were studied because of the relatively primitive condition of the structure. Other members of the Parasitica were examined, and studies were made of examples of the two orders of the [illegible], the [illegible] and Lepidoptera.

2. TERMINOLOGY

The terminology used is that of Snodgrass (1928, 1935, 1947, 1950) with the minor alterations which I have given in a recent paper (Short, [illegible]). Muscles have been given numbers corresponding with those given to their counterparts in Orthoptera by Snodgrass (1928).

Kloet and Hincks (1945) have been followed in nomenclature.

3. INTERRELATIONSHIPS OF THE SYMPHYTA, PARASITICA AND ACULEATA

Little is known concerning the origin of the Hymenoptera. The Symphyta are the most primitive Hymenoptera. From a study of the Symphyta, Ross ([illegible]) finds evidence indicating that the extinct Xyelidae link the Hymenoptera to a Mecopteroid ancestor. This author believes that the Orussidae link the Symphyta to the parasitic Hymenoptera. He states (p. [illegible]): "The Orussidae, which are accepted as the most primitive family of the Apocrita, apparently arose from a Siricid ancestor."

There is, however, no agreement as to which family of the Apocrita is the most primitive (see Handlirsch, [illegible]; Ross, [illegible]; Tillyard, [illegible]; Telenga, [illegible]). Wheeler ([illegible]) believes that the Trigonalidae should be placed near the point of divergence of both Parasitica and Aculeata from the ancient Symphyta (see also [illegible], [illegible]). Wheeler suggests that the early Vespoidea and Sphecoidea arose among the Bethyloidea. The latter, [illegible] in the [illegible], [illegible] [illegible] ancestors. He derives the social Vespidae and Formicidae from primitive Vespoidea.

Certain features of behaviour which are prominent in the Aculeata may be recognised in the Symphyta. *Orussus* is parasitic, and some other sawflies are [illegible]. Parthenogenesis is known, as are [illegible] and [illegible] (Wheeler, [illegible]). It is significant that the Oryssidae, [illegible], [illegible] and many primitive Vespoidea and Sphecoidea are parasites of wood-boring insects (see [illegible], [illegible]).

It is impossible to make a rigid distinction between the Parasitica and Aculeata on the structure of the adults or the larvae. Vandel ([illegible]) has recently that the heads of the externally feeding Parasitica are little different from those of internal predators such as the Siricidae.

---

[1] The concept of homology has been much discussed in recent years (see [illegible], [illegible]; Remane, [illegible]). It is generally agreed that the best criterion for homology is comparative anatomy.

4. THE HEAD OF SYMPHYTA.

Parker (1934) has described the anatomy of the Tenthredinoid head. His account is unsatisfactory in the following points:

a. The mala and lacinia are confused.

b. The epistomal suture and the frontal arms of the dorsal ecdysial cleavage line are confused.

c. The relationship of the labial muscles to the labial sclerites is not stated.

d. The hypostomal suture is misinterpreted.

e. Homologies between the muscles of the Tenthredinid head and the Orthopteroid head are often not stated.

f. The homologies of the proximal and distal sclerites of the stipes are confused.

It was therefore necessary to make a detailed examination of a member of the Symphyta. The heads of the adults of the Siricidae and Xiphydriidae were studied since these approach the parasitic Orussidae in structure (Yuasa, 1922). It was not thought necessary that the head of a feeding larva should be studied in detail. The claim that the Apocrita had a Tenthredinid ancestor is based on the assumption that the Tenthredinidae are the most primitive family of the Apocrita. The evidence for this claim is not conclusive.

In the diagrams of the head of Xiphydria (fig. 1) membranous areas are shown in stipple, lightly sclerotized areas are left unshaded and heavier areas of sclerotization are indicated by shading. (Areas of sclerotization can easily be seen, since hard sclerotized cuticles are always dark (Wigglesworth, 1939).) This scheme of shading is not used in the remaining diagrams.

a. The Cranium (fig. 1).

The head of Xiphydria is partially prognathous and sclerotization is reduced. The cranium of Xiphydria is not very different from a primitive Symphytan such as Pamphilius (fig. 10).

In Pamphilius the strengthening ridges (epst, pst) which surround the mouth parts are conspicuous. In Xiphydria the mandibles well, the cranial areas (epst, pst) surrounding the mouth parts and the ridge of the occipital sulcus (os) are the most strongly sclerotized parts of the cranium.

(The structure called the occipital sulcus and ridge is not a definite infolding of the cranium. It is merely a thickening and sclerotization of the cranial wall. However since it is a strengthening bar in the position of the strengthening sulcus and ridge of Orthopteroids it may be homologized with this structure. This is not an extreme interpretation, since the occipital sulcus and ridge of Orthopteroids is not a pronounced infolding. It is little more than a thickening of the postero-lateral cranial wall.)

Where the ridge of the epistomal sulcus (fig. 1, es) is externally visible as in Pamphilius and Xiphydria, it may be called the epistoma (fig. 1, epst). There are no precise pleurostomal areas between the mandibular articulations as in Orthopteroids, but there are internal ridges (fig. 1, pr) on the cranial wall.

between the articulations. These pleurostomal ridges are visible externally. The external cranial area of each ridge may be called a pleurostoma (fig. 1, *plst*). Hypostoma (*hst*) may be used in a similar sense for the external cranial area of the hypostomal ridge (fig. 2, *hr*).

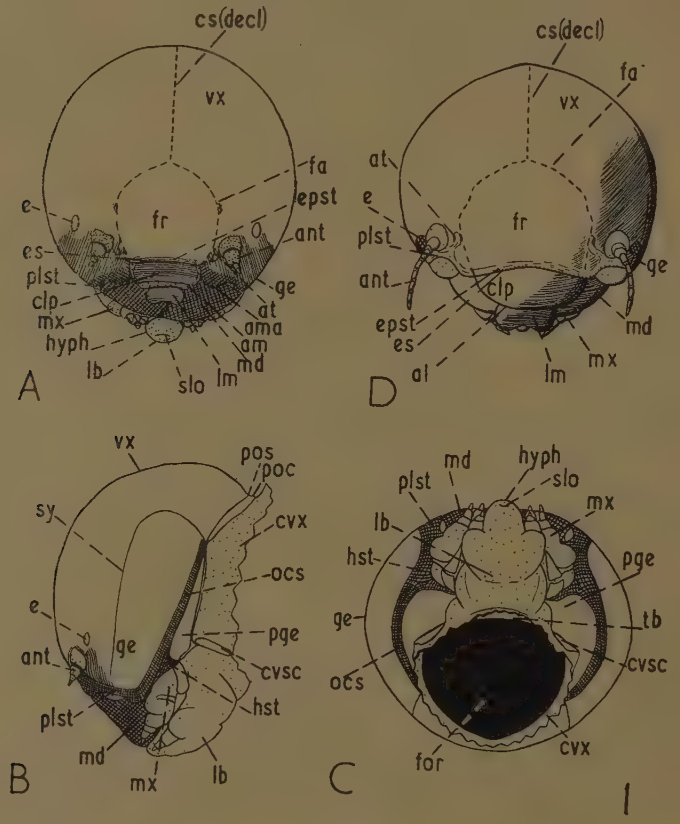
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Fig. 1.—A. Anterior view of head of *Xiphydria camelus* (L.). B. Lateral view. C. Posterior view. D. Anterior view of *Pamphilius pallipes* (Zett.).

A pair of sulci (fig. 1, *sy*) extend from the post-occipital sulcus (*pos*) over the occipital and parietal areas. Parker (1934) calls these sulci post-temporal. This name is not followed since the name temporal is not used to describe a cranial area in Snodgrass's description of the basic Pterygote head. When a structure without apparent homologies is found only within the narrow limits of a group it is not necessary to give a term. A descriptive phrase such as is given above is sufficient.

b. *The Tentorium* (fig. 2B).

This has the same form as that of Orthopteroids.

c. *The Hypopharynx.*

The hypopharynx (fig. 1, *hyph*) of Hymenopterous larvae is united with the maxillae (*mx*) and the labium (*lb*) to form an under-lip complex.

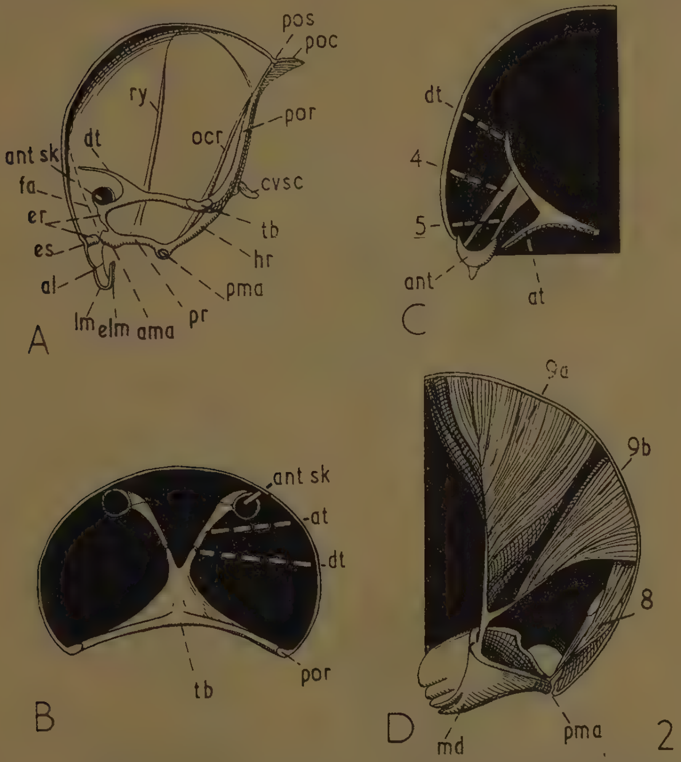
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FIG. 2.—A. Lateral view of longitudinal section of head capsule of *Xiphydria camelus* (L.). B. Dorsal view of tentorium of *X. camelus* (L.). C. Posterior view of muscles of left antenna of *Sirex cyaneus* F. D. Posterior view of muscles of right mandible of *S. cyaneus* F.

In *Xiphydria* and *Sirex* the anterior part of the hypopharynx has become enclosed within the head cavity in correlation with the trend towards a hypognathous head (*see* fig. 3B). This enclosure is deduced from two features:

i. Part of the suspensorium of the hypopharynx (*sh*) now lies beneath the anterior part of the stomodaeum.

ii. The clypeal muscles (33, 34) indicate that part of the cibarium has been enclosed within the head cavity.

The basal sclerites of the hypopharynx (*bsh*) are present. These give origin to the dorsal muscles of the salivarium (fig. 5, 1*s*).

d. *The Appendages.*

i. The antennae and antennal muscles are reduced (fig. 2C).

ii. The mandibles and mandibular muscles are well developed (fig. 2D).

iii. The maxillae (fig. 4) are reduced. The maxillae of *Xiphydria* are not markedly different from those of *Pamphilius* (fig. 4D). The sclerotization is

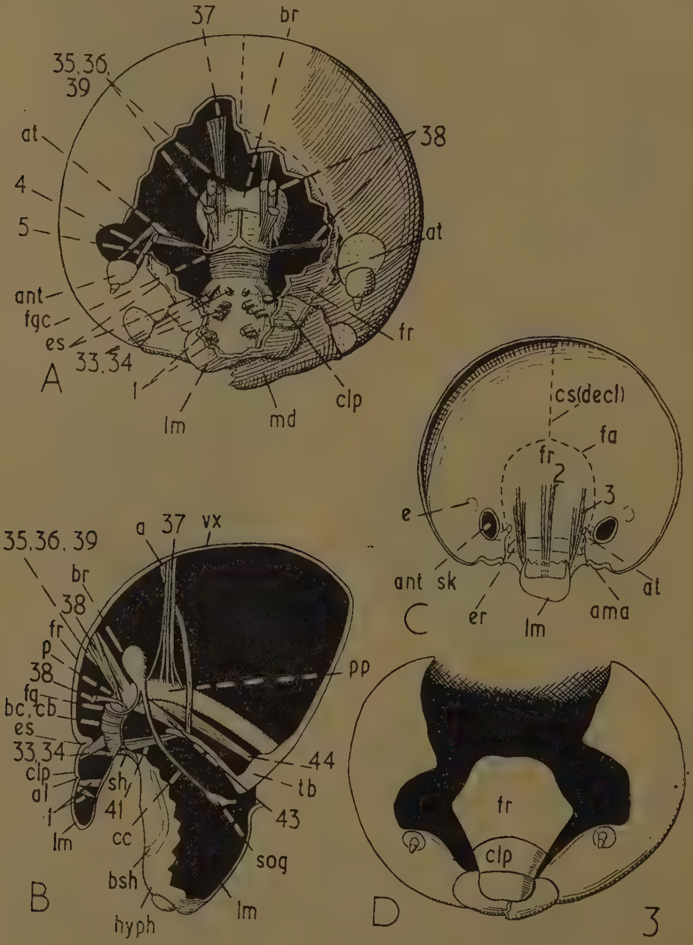
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Fig. 3.—A. Anterior view of dissection of *Sirex cyaneus* F. B. Lateral view of dissection of *S. cyaneus* F. C. Posterior view of cranium of *Xiphydria camelus* (L.) showing labral muscles. D. Exuviae of last larval instar of *Sirex* sp.

weaker. The galea (fig. 4A, *ga*) has become more palp-like and the maxillary palp (*mplp*) is reduced.

The cardo (*cd*) of *Xiphydria* has a slender promotor muscle (10) and three muscles representing the adductors (11).

The sclerotized part of the stipes (*st*) is reduced to a thin strip on the posterior surface of the maxilla. Muscles having origin and insertion on the stipes are confined to this strip. It may therefore be regarded as representing the ridge *sr* (*q* of Snodgrass) of the stipes of Orthopteroids. Three muscles (12, 13*a*) which have origin on the anterior tentorial arms insert on the stipes. These correspond to the proximal and first distal adductors of the stipes of Orthopteroids.

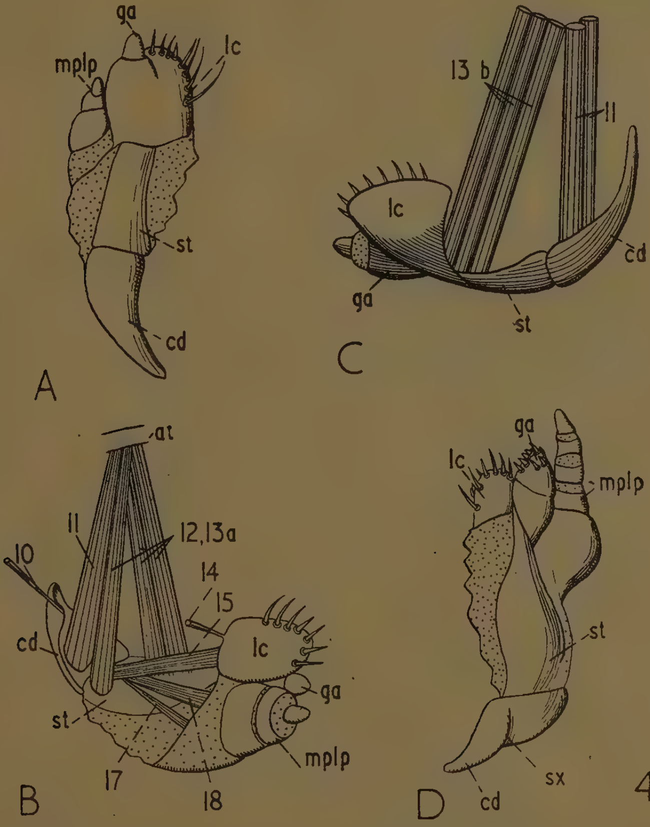

FIG. 4.—A. Posterior view of right maxilla of *Xiphydria prolongata* (Geoff.). B. Anterior view of right maxilla of *X. prolongata* dissected to show muscles. C. Median and posterior view of maxilla of *X. prolongata* dissected to show muscles. D. Posterior view of right maxilla of *Pamphilius pallipes* (Zett.).

The lacinia (*lc*) possesses stipital (15) and cranial (14) flexors.

The galea (*ga*) has no muscles.

The palp (*mplp*) has a stipital depressor (18) and levator (17) but palpal muscles are absent. (Palpal muscles are present in *Pseudoclavellaria* (Parker, 1934)).

iv. The labium (fig. 5) of all Symphytous larvae is weakly sclerotized (see *Pamphilius*, fig. 5B). In *Xiphydria* (fig. 5A) and *Sirex* (fig. 5C) it is still possible to distinguish generally the limits of the postlabium. (The labium in *Sirex* and *Xiphydria*, although membranous, has not been stippled in fig. 5.)

The ligula (glossae and paraglossae) of the sawfly labium is fused with the hypopharynx to form a terminal lobe. The duct of the labial glands (*slo*) opens on the apex of this lobe.

The labial muscles are as follows:

Posterior or ventral retractors of the prementum (23).
Anterior or dorsal retractors of the prementum (24).
Dorsal muscles of the salivarium (1*s*).
Median muscles of the labium (*rst*).

A pair of muscles (*b*) has origin on the dorso-lateral edges of the postoccipital ridge and insertion on the posterior end of the basal sclerite of the hypopharynx. Parker (1934) has found these muscles in *Cephus* and *Pseudoclavellaria*. He calls them the dorsal (proximal) retractors of the prementum. This name indicates the function of these muscles but not the homologue in Orthopteroids. Das (1937) calls them the cranial flexors of the prementum. He thinks that they represent the tergal muscles of the labial appendages. This interpretation is not accepted. The labium of larval Symphyta is obviously specialized. In Orthopteroids the labium has no cranial muscles.[2] In adult bees labial adductors arise on the cranium, but the condition is a secondary one given by a migration of the muscle bases from the tentorial bar to the adjacent walls (Snodgrass, 1942). It is possible that this pair of muscles (*b*) of Symphytous larvae is homologous with the retractors of the hypopharynx (32) of Orthopteroids. The bases of these muscles may have migrated from the tentorial bar to the postoccipital ridge.

Retractors of the palps are absent in *Sirex*. They are present in *Xiphydria*.

Palpal muscles are absent in both *Sirex* and *Xiphydria*. They are present in *Pseudoclavellaria* (Parker, 1934).

5. THE HEAD OF ICHNEUMONOIDEA.

i. The Head of ICHNEUMONIDAE, BRACONIDAE and AGRIOTYPIDAE.

The specializations which have been noted in the Symphyta are more pronounced in the heads of Ichneumonid, Braconid and Agriotypid larvae. The head is more prognathous. Sclerotization is further reduced, but the epistoma, pleurostoma and hypostoma are usually distinct. Sclerotic bars are also present on the maxillae and labium. The antennae, maxillae and labium are further reduced.

Vance and Smith (1933) and Beirne (1941) have listed the various interpretations which have been made of the structure of the larval head of parasitic Hymenoptera.

[2] Following Snodgrass's interpretation. Cf. Weber (1949).

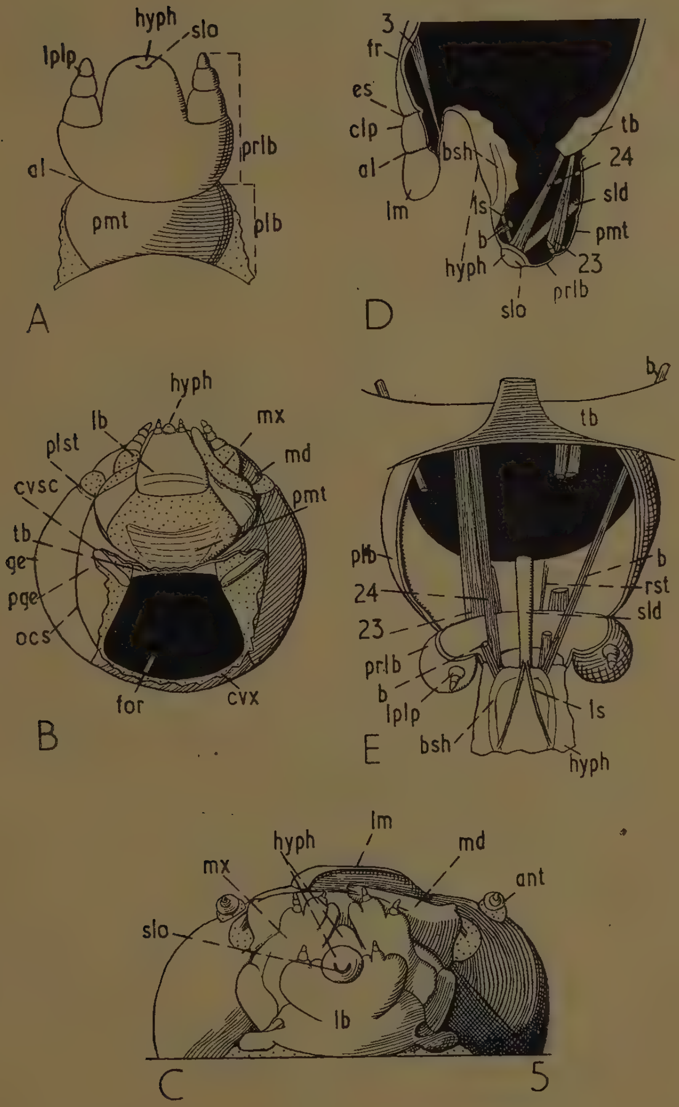
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FIG. 5.—A. Posterior view of labium of *Xiphydria camelus* (L.). B. Posterior view of head of *Pamphilius pallipes* (Zett.). C. Posterior view of head of *Sirex cyaneus* F., showing association of maxillae, labium and hypopharynx. D. Lateral view of dissection of *S. cyaneus* F., showing muscles of labrum and labium. E. Anterior view of dissection of labium of *S. cyaneus* F.

In this account Snodgrass's criteria have been followed in interpreting the structure of the cranium and appendages. To apply these criteria it was necessary to investigate the structure of the nervous and muscular systems in a selected type. Studies have been made of these systems in Braconids (Grandori, 1911; Genieys, 1925; Parker, 1931; Vance, 1932) and in an Ichneumonid (Smith, 1932). In no case is the account complete and muscle homologies have not been attempted. The present interpretation is based on the study of an ectoparasitic Ichneumonid *Xorides* sp.

a. *The Cranium.*

The word cranium is substituted for epicranium in this account (cf. Vance and Smith). If the word epicranium is used at all it should be applied only to the upper part of the cranium.

In Braconids and Ichneumonids the mature larva differs from the earlier instars in that the frontal arms of the dorsal ecdysial line are not present. (See fig. 9 for the position of the cleavage line in a fourth and fifth instar Ichneumonid.) This difference has been noted by Glover (1934) in *Bracon*. The structures in the larvae of the Apocrita which previous authors (e.g., Snodgrass, 1947) have regarded as remnants of the frontal arms of the cleavage line are grooves (fig. 6, *dfm*) marking the positions on which the precerebral pharyngeal (fig. 7, 35, 36, 39), dorsal hypopharyngeal (38) and labral retractor muscles (2, 3) have origin.

The clypeus (fig. 6, *clp*) of *Xorides* is not marked off from the frons (*fr*) by a complete epistomal arch (*epst*). In most Braconids of the subfamily Braconinae and in Ichneumonids of the subfamilies Ichneumoninae and Orthopelminae (of Beirne) the epistomal arch is complete. Where the epistomal arch is incomplete the cibarial muscles (fig. 7, 33, 34) identify the clypeal area. Vance and Smith indicate the anterior (ventral) limit of the clypeus by a dotted (and presumably hypothetical) line between the anterior tentorial pits (fig. 6, *at*). A study of the labral musculature indicates that the labral sclerite[3] (*lms*) shows the limits of the labrum (*lm*).

The temporal and antennal cranial regions of Vance and Smith are not indicated. It is impossible to define these areas, and it was not found necessary to describe them when studying the basic Pterygote head.

The structure which Vance and Smith call the "temporal suture" is a groove above the region where the compound eye develops (see *Vespula*, fig. 24D). Parker (1943) describes this groove in *Polistes* and calls it an "ocular fossa." The word fossa is suitable for this structure only when it is a deep groove as in Vespid larvae. In most of the larvae of the Apocrita the groove is slight. This groove has no obvious strengthening function and therefore cannot be called a sulcus. This structure above the eye is here called the ocular line (fig. 6, *ol*).

The processes of the pleurostoma (*plst*) with which the mandibles (*md*) articulate are here called anterior and posterior, not dorsal and ventral as given by Vance and Smith. The purpose of this is to use a terminology similar to that applied to the basic Pterygote head. The word process is used in place of ramus since ramus (L. *ramus*, a branch) infers an elongate structure

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[3] Vance and Smith refer to the various sclerotized parts of the head as scleromes. Snodgrass (1935 : 81) uses the word scleroma for the sclerotic annulus of a body segment. He uses the word sclerite for a sclerotized area of the body wall. Snodgrass's terminology is followed here.

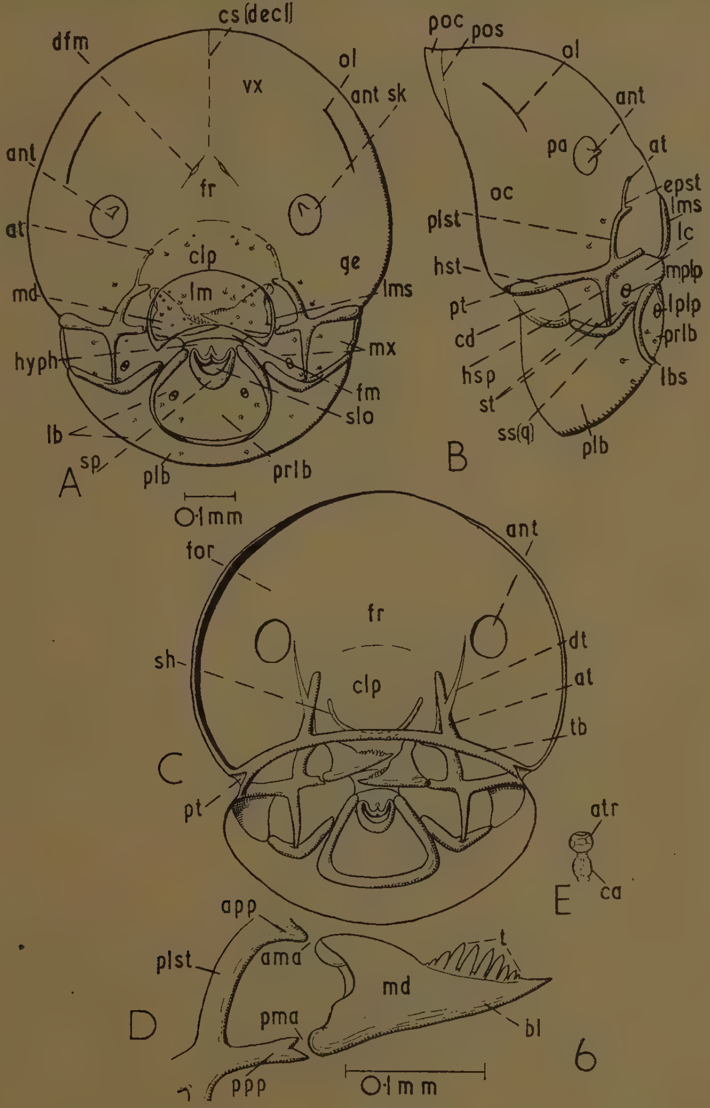
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Fig. 6.—The head of *Xorides* sp. (Ichneumonidae: Xoridini). A. Anterior view. B. Lateral view. C. Posterior view of head capsule showing tentorium. D. Anterior view of mandible. E. Spiracle.

such as a nerve branch. These projections of the pleurostoma are therefore called anterior and posterior pleurostomal processes (*app, ppp*).

b. *The Tentorium* (fig. 6c).

Snodgrass's terminology is used here in preference to that of Vance and Smith. The body of the tentorium is absent and the anterior arms (*at*) arise separately from the tentorial bar (*tb*) (cf. Orthopteroids and Symphyta). Vance and Smith figure the dorsal tentorial arm as attached to the "frontal suture." In *Xorides*, *Gasteruption*, *Bombus* and *Vespula* the dorsal arms of the tentorium are attached to the cranium slightly mesad of the antennae. It is probable that the dorsal arms have this position in all the larvae of the Apocrita. This is not strange, for the antennal muscles of Pterygotes usually arise from the dorsal arms of the tentorium. The dorsal tentorial marks (*dtm*) are not distinct in *Xorides*, but they may be seen in *Gasteruption* (fig. 11B), ***Bombus*** **(fig. 18A) and** ***Vespula*** **(fig. 22A).**

c. *The Hypopharynx.*

The hypopharynx (fig. 6, *hyph*) is fused with the maxillae (*mx*) and labium (*lb*) to form an under-lip complex. As with *Sirex* and *Xiphydria*, the anterior part of the hypopharynx has become enclosed within the head cavity in correlation with the formation of a hypognathous head. The suspensorial sclerite of the hypopharynx (fig. 7A, *sh*) may be recognized as a thickening of the intima to which are attached the dorsal hypopharyngeal muscles (38). This resembles the condition in *Sirex* (fig. 3). The dorsal muscles (fig. 7, 18) of the silk press (*sp*) also have origin on the suspensorium.

The suspensorial sclerite is shown in fig. 6c since it is often visible in cleared mounts. Thorpe (1930) figures it in *Orgilus* and calls it the pharyngeal trough.

Vance and Smith label the structure which is here called the hypopharynx as the "glossa." They state that this "glossa" is equivalent to the anterior part of the hypopharynx. This interpretation is not understood. The area of the labium-hypopharynx which is situated above the orifice of the silk press (fig. 6, *slo*) and between the maxillae (*mx*) is clearly the entire hypopharynx. The term glossae is usually given (Snodgrass, 1935 : 155) to the two median ligular lobes of the labium.

d. *The Appendages.*

i. The mandibles (fig. 6, *md*): It is not considered necessary to use the terms mandibular condyle and mandibular acron of Vance and Smith. It is sufficient to differentiate the anterior (*ama*) and posterior (*pma*) mandibular articulations.

ii. The maxillae (fig. 6, *mx*): The interpretation here differs completely from that of Vance and Smith.

The cardo (*cd*) is present as a more or less definite sclerotic plate in many Braconid and in at least some Ichneumonid larvae (some Ephialtini, Ophionini, Xoridini). This interpertation agrees with that of Grandi (1931), Goidanich (1933) and Russo (1938). The tentorial adductor of the cardo is present (fig. 8, 11).

Most of the remainder of each maxilla may be regarded as the stipes (fig. 6, *st*). However, on the terminal lobe of each maxilla is inserted a muscle (fig. 8, 14) which has origin on the postero-lateral cranial wall. These muscles

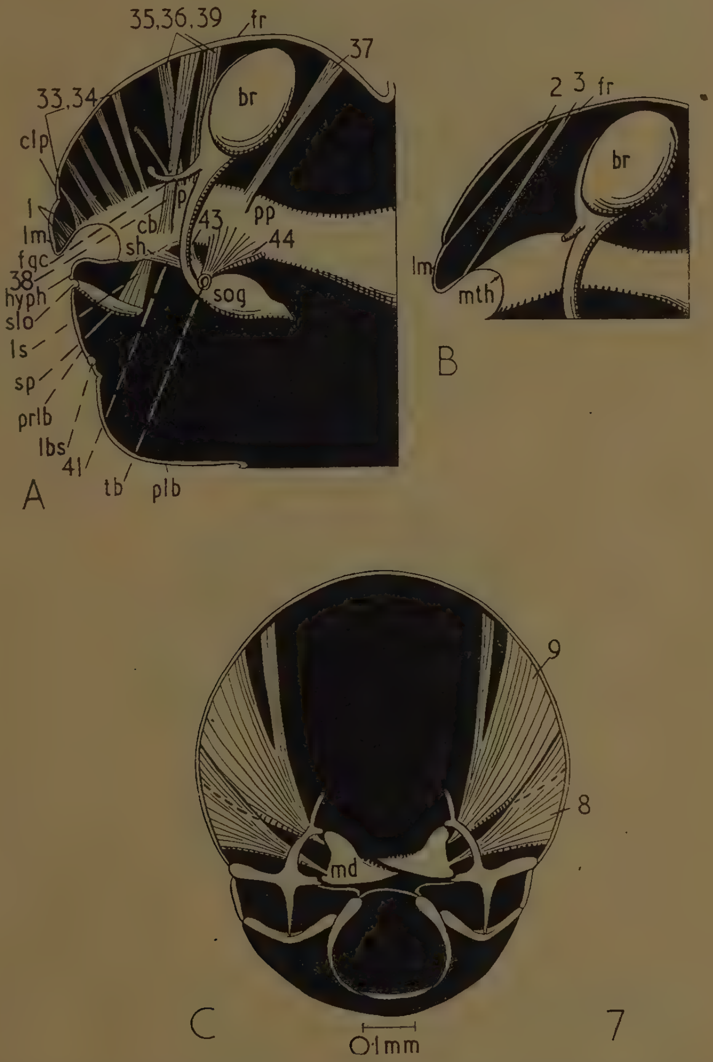
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FIG. 7.—The head of *Xorides* sp. (Ichneumonidae : Xoridini). A. Lateral view of head drawn as a dissected object. B. Lateral view of head drawn as a dissected object to show labral retractors. C. Anterior view of head drawn as a dissected object to show mandibular muscles.

may be homologized with the cranial flexors of the laciniae. The medial lobe of each maxilla may therefore be regarded as a lacinia (fig. 6, *lc*).

The galea is lacking. (The galea is reduced in *Sirex* and *Xiphydria*).

The maxillary palps (*mplp*) are represented by flat discs.

The sclerotic bar (*ss*(*q*)), which extends from the cardo along the posterior edge of the maxilla, is homologous with the sclerotized part of the stipes in *Xiphydria* (fig. 4). It is also homologous with the sulcus and ridge of the stipes of Orthopteroids. This bar (*q* of Snodgrass, 1928) may therefore be called the stipital sclerite.

A sclerotic spur (fig. 6, *hsp*) extends from the hypostoma (*hst*) across the membranous part of the stipes to the stipital sclerite. Vance and Smith call this spur the " stipital sclerome," and suppose that it divides the maxilla into a lateral cardo and a medial stipes. This suggestion is not supported by the available evidence. Their term is best used, as above, to describe another structure. The most suitable term is sclerotic spur of the hypostoma as given by Snodgrass (1935 : 297). The sclerotic spur of the hypostoma apparently exists only in Ichneumonids, Braconids and Agriotypids. Folds occur in the stipes of *Gasteruption* (fig. 11) and *Bombus* (fig. 18), but these are not sclerotized. The hypostomal spur has no homologue in Orthopteroids or in the Symphyta.

iii. The labium consists of two parts, the prelabium (fig. 6, *prlb*) and the postlabium (*plb*). Vance and Smith think that the labium is divided into these parts by the labial sclerite (*lbs*). This interpretation is questioned, for it is doubtful that the labial sclerite is homologous with the articular line which separates the pre- and postlabium of Orthopteroids. The labial sclerite is here regarded as a marginal sclerotization of the prelabium. This conclusion agrees with that of Snodgrass (1935).

Vance and Smith indicate a ligular region and a labiostipites (prementum) of the prelabium. The components of the prelabium of Orthopteroids are the terminal lobes (ligula), the prementum and the palps. The terminal lobes and the prementum cannot be differentiated in Hymenopterous larvae. It is therefore preferable to call the area within the labial sclerite and below the orifice of the silk press the prelabium. Beirne (1941) calls this area the prementum. This is not accepted, since the term prementum is applicable only to the stipital region of the prelabium and does not include the ligula and palpi.

Vance and Smith describe a " ligular sclerome " in the " ligular region " of the prelabium. Authors generally have confused this " ligular sclerome " with the silk press (fig. 6, *sp*) which is a thickening of the wall of the median duct of the silk glands. The silk press has been described as a sclerite presumably because it is visible through the thin body-wall. A Y-shaped sclerotic area is present on the prelabium of some Ichneumonids (e.g., *Banchus*) and is distinct from the silk press. When this Y-shaped sclerotic area is present it may be called a prelabial sclerite. The prelabial sclerite has not been seen in any Braconid.

The part of the labium posterior to the stipital and labial sclerites is the postlabium (*plb*). Beirne (1941) calls this area the postmentum. According to Snodgrass's terminology, postmentum and postlabium are interchangeable terms. The word postlabium is used in this study in preference to postmentum since this gives a uniform nomenclature to the labium. Further, it is necessary to make some distinction between a postlabium which is entirely membranous and a postlabium which is partly sclerotized (cf. *Locusta*, *Pamphilius*, fig. 5B, and *Xorides*, fig. 6). It is recommended that the word postlabium be used for the entire area posterior to the articular line between the pre- and postlabium, and that the word postmentum or postmental sclerite be restricted to the sclerotized area (if present) of the postlabium.

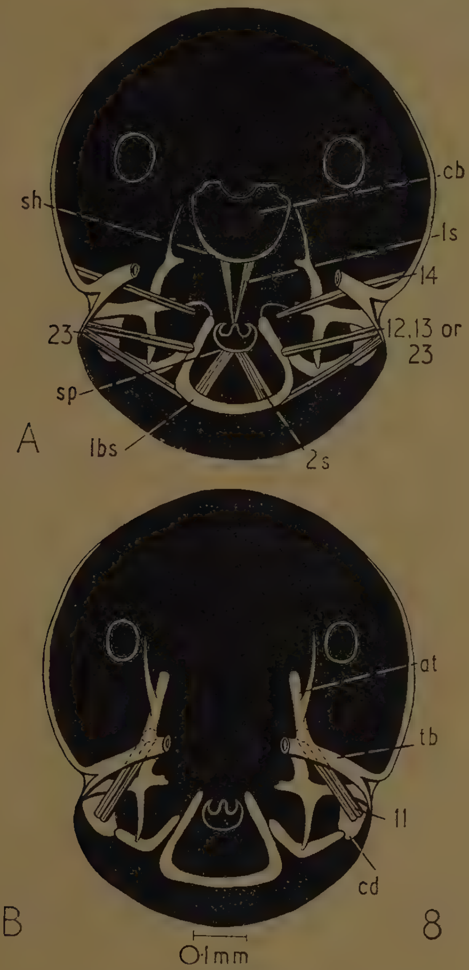

FIG. 8.—The head of *Xorides* sp. (Ichneumonidae: Xoridini). A. Posterior view of head drawn as a dissected object to show maxillary and labial muscles. B. Posterior view of head drawn as a dissected object to show adductors of the cardo.

The muscles of the labium are as follows:

1. The salivary muscles of the labium (fig. 8, 2*s*) have origin on the labial sclerite and insertion on the silk press.

2. Two pairs of muscles (12, 13 or 23 and 23) have origin on the thickened posterior edge of the postlabium close to the tentorial bar (*tb*) and insertion on the labial sclerite. Both pairs of muscles are probably homologous with the posterior or ventral retractors of the prementum (23) of Orthopteroids and Symphyta. However, since the anterior pair of muscles inserts on the labial sclerite on the point of articulation of this and the stipital sclerite, it may represent the stipital adductors (12, 13) of Orthopteroids and Symphyta. These two pairs of muscles are described in *Macrocentrus* by Parker (1931) and in *Chelonus* by Vance (1932).

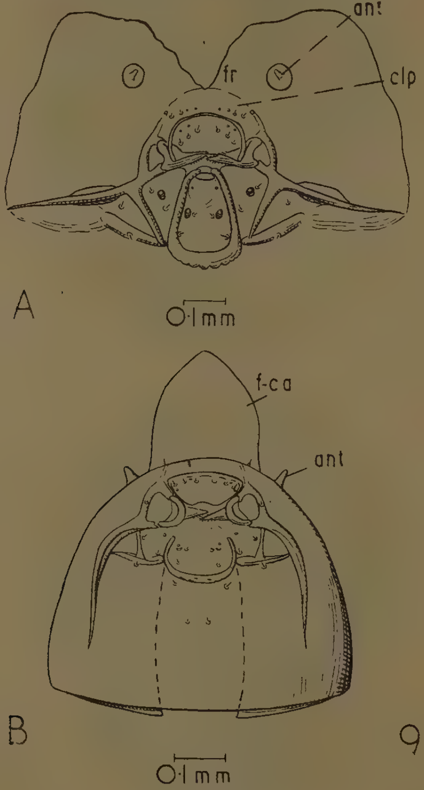

Fig. 9.—Exuviae of head of Ichneumonid (Ephialtini). A. Fifth instar. B. Fourth instar.

The two pairs of muscles inserted on the labial sclerite apparently serve to retract the base of the prelabium and thereby evert the orifice of the silk press. The labial sclerite would rotate on the extremities of the stipital sclerites. The stipital sclerite (which articulates with the labial sclerite) and the spur of the hypostoma (which articulates with the stipital sclerite) probably serve to hold the maxilla rigid during this process. In general, the spinning apparatus of Hymenopterous larvae resembles that of caterpillars (see Snodgrass, 1928).

e. *Setae and Sensilla.*

On the head are various setae and sensilla which may be useful in taxonomy.

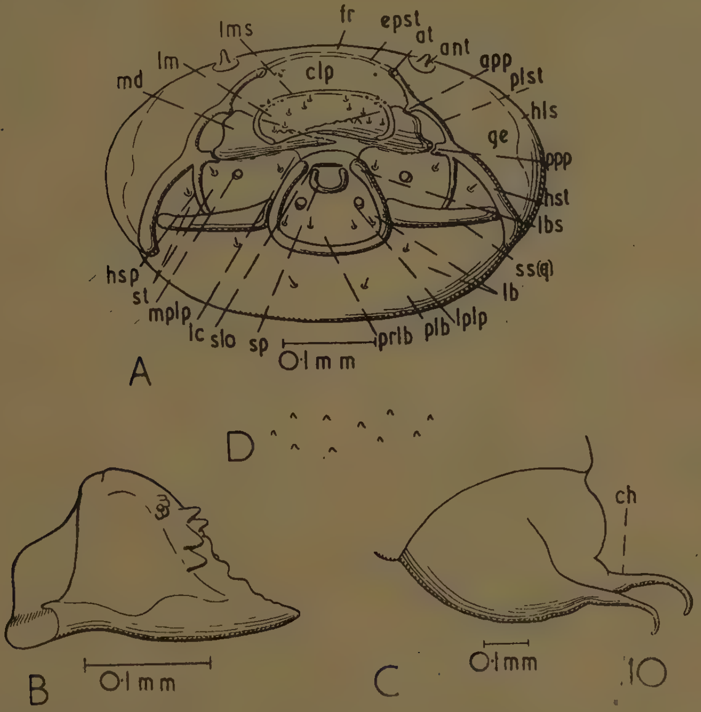

Fig. 10.—Larva of *Agriotypus armatus* Curtis (Agriotypidae). A. Anterior view of head. B. Antero-dorsal view of mandible. C. Lateral view of caudal segment showing caudal hooks. D. Skin. Definite spiracles are not present.

They may be referred to according to position, e.g., clypeal, labral, pre- and postlabial. The setae on the stipes of the maxilla may be called inner or outer according as they lie mesad or laterad of the spur of the hypostoma.

f. *The Food Meatus.*

Vance and Smith call the cavity which is bounded laterally by the laciniae, anteriorly by the labrum and posteriorly by the hypopharynx the " preoral cavity." This is unusual, for preoral cavity is usually applied to the extra-oral cavity, which is bounded by the labrum and mouth appendages as in Orthopteroids. The hypopharynx lies within the preoral cavity. This oral cavity of the larvae of the Apocrita is more accurately called the food meatus (fig. 6, *fm*).

g. *Membrane and Sclerite.*

Morphologists have, in the past, made their descriptions of insect morphology a series of descriptions of sclerites. It has already been stressed that this practice has raised difficulties in the nomenclature of the labium.

A similar instance may be seen with the cardo of the maxilla. This was first defined as a sclerotic area. Later it was emphasized that characteristic muscles insert on this sclerite. In *Xorides* both the sclerite and the tentorial adductors are present. But in *Macrocentrus* (Parker, 1931), where the sclerite is absent, the tentorial adductor is inserted on the membranous area at the base of the maxilla. Is the cardo present in *Macrocentrus ?*

h. *Summary of Interpretations.*

Vance and Smith.	**Beirne.**	**Present interpretation (*see* fig. 6).**
antenna	antenna	antenna (*ant*)
antennal foramen	antennal socket	antennal socket (*ant sk*)
antennal region	?	not differentiated. Merely part of the parietals (*pa*) of cranium
anterior tentorial pit	anterior tentorial pit	anterior tentorial pit (*at*)
anterior tentorial ramus	anterior tentorial ramus	anterior tentorial arm (*at*)
clypeus	clypeus	clypeus. Note that the limits differ from those given by Vance and Smith
dorsal tentorial mark	dorsal tentorial mark	depression marking place of origin of frontal muscles (*dfm*)
dorsal tentorial ramus	dorsal tentorial ramus	dorsal arm of tentorium (*dt*)
epicranium	epicranium	cranium
epistoma	epistoma	epistoma (*epst*)
foramen magnum	?	foramen magnum (*for*)
frons	frons	frons (*fr*). The limits differ from those given by Vance and Smith
frontal sutures	?	grooves associated with depressions (*dfm*) which mark the positions of the frontal muscles
genal region	genal region	genal region (*ge*)
glenoid fossa	?	part of the posterior mandibular articulation (*pma*)
glossa	?	hypopharynx (*hyph*)
hypostoma	hypostoma	hypostoma (*hst*)
inferior pleurostomal ramus	inferior pleurostomal ramus	posterior pleurostomal process (*ppp*)
labial palp	labial palp	labial palp (*lplp*)

Vance and Smith.	Beirne.	Present interpretation (*see* fig. 6).
labial setae	labial setae	labial setae
labiobase	postmentum	postlabium (*plb*)
labiostipital sclerome	labial sclerome	labial sclerite (*lbs*)
labium	labium	labium (*lb*)
..	labral sclerome	labral sclerite (*lms*)
labrum	labrum	labrum (*lm*)
ligular region and labiostipites	prementum	prelabium (*prlb*)
ligular sclerome	ligular sclerome	prelabial sclerite
mandible	mandible	mandible (*md*)
mandibular acron	?	part of the anterior mandibular articulation (*ama*)
mandibular condyle	?	part of the posterior mandibular articulation (*pma*)
maxilla	maxilla	maxilla (*mx*). Note that the interpretation of this appendage differs from that of Vance and Smith
maxillary lobe	maxillary lobe	lacinia (*lc*)
maxillary palp	maxillary palp	maxillary palp (*mplp*)
maxillary sclerome	maxillary sclerome	stipital sclerite (*ss*(*q*))
maxillary setae	maxillary setae	maxillary setae
metopic suture	metopic suture	coronal stem of dorsal ecdysial cleavage line *cs* (*decl*)
orifice of silk duct	orifice of silk duct	orifice of silk press (*slo*)
papillus	sensorium	sensillum
pleurostoma	pleurostoma	pleurostoma (*plst*)
preoral cavity	preoral cavity	food meatus (*fm*)
posterior tentorial pit	posterior tentorial pit	posterior tentorial pit (*pt*)
postocciput	?	postocciput (*poc*)
postoccipital suture	?	postoccipital sulcus (*pos*)
superior pleurostomal ramus	superior pleurostomal ramus	anterior pleurostomal process (*app*)
stipital sclerome	stipital sclerome	sclerotic spur of hypostoma (*hsp*)
temporal suture	temporal suture	ocular line (*ol*)
temporal region	temporal region	not differentiated. Merely part of parietals (*pa*) of cranium
transverse tentorial bar	transverse tentorial bar	tentorial bar (*tb*)
vertex	vertex	vertex (*vx*)

ii. The Head of Evaniidae.

Gasteruption assectator (L.) is studied as a type (figs. 11–14).

Gasteruptioninae.—The head of *Gasteruption* differs from the type common to Ichneumonids, Braconids and Agriotypids in that the stipital and labial sclerites and the sclerotic spur of the hypostoma are lacking. The epistoma is not well developed. The large tridentate mandibles (*md*) differ in form from the more slender mandibles of Ichneumonids and Braconids.

EVANIINAE.—Judging from Geniey's (1924) description of *Zeuxevania*, there do not appear to be any major differences between the morphology of the head in Evaniinae and Gasteruptioninae.

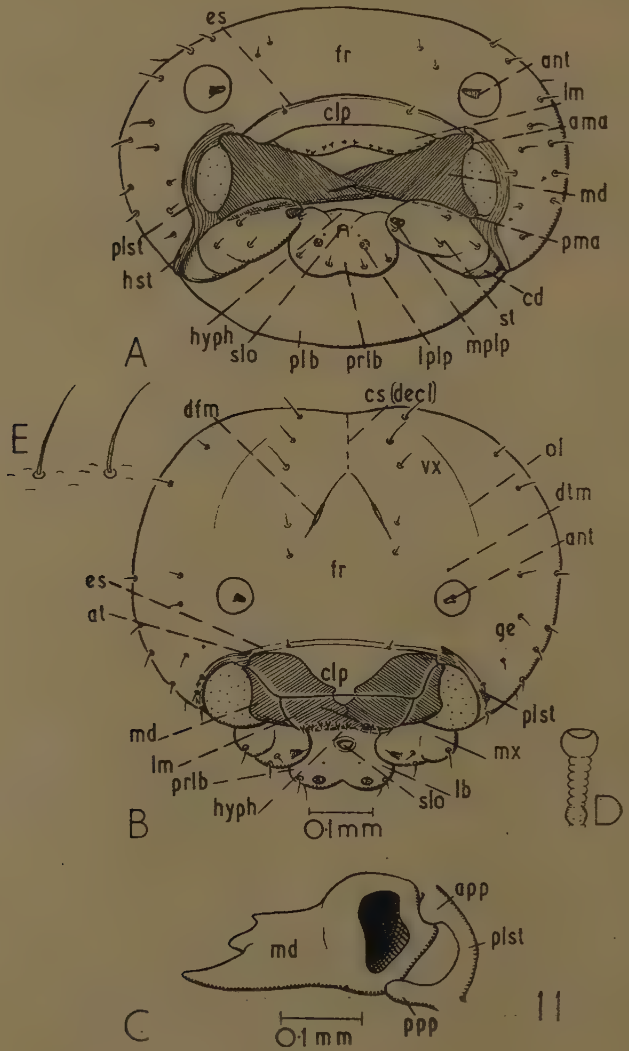
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FIG. 11.—The head of *Gasteruption assectator* (L.) (Evaniidae). A. Antero-ventral view. B. Anterior view. C. Posterior view of mandible. D. Spiracle. E. Skin.

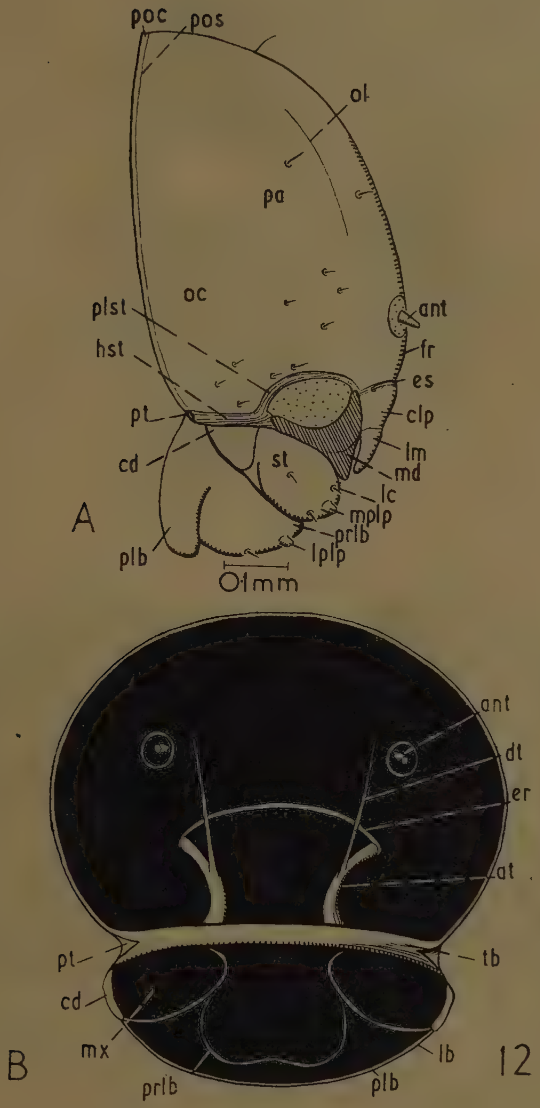
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FIG. 12.—The head of *Gasteruption assectator* (L.) (Evaniidae). A. Lateral view. B. Posterior view of head capsule showing tentorium.

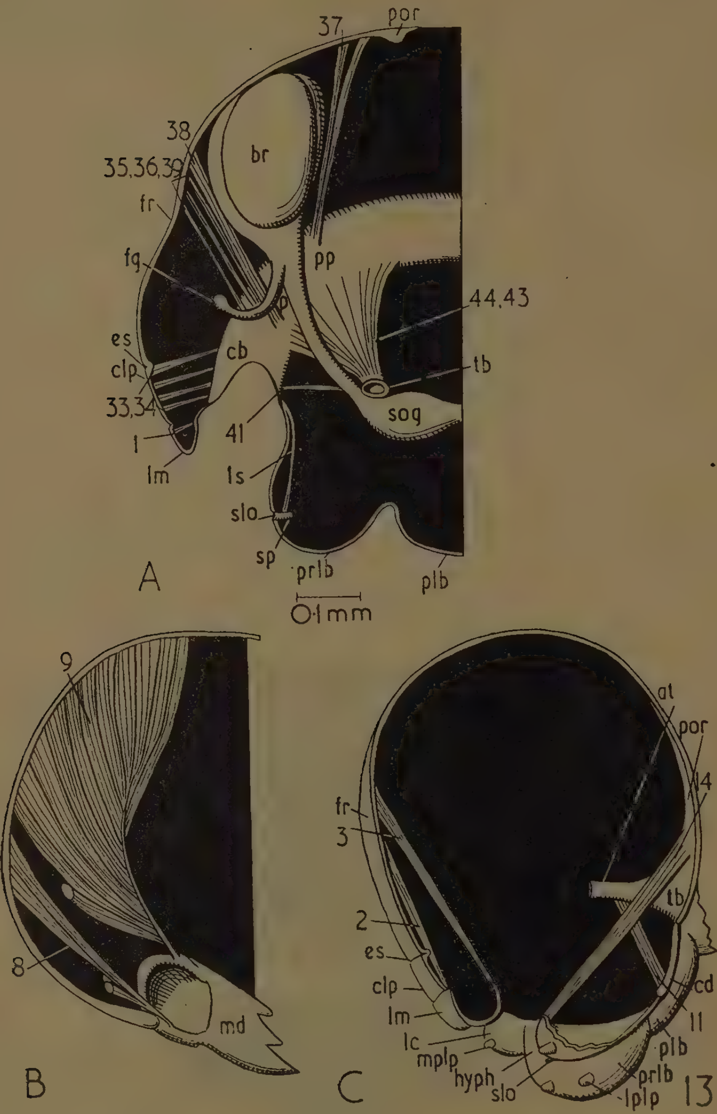
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FIG. 13.—The head of *Gasteruption assectator* (L.) (Evaniidae). A. Lateral view of head drawn as a dissected object. B. Anterior view of head drawn as a dissected object to show mandibular muscles. C. Antero-lateral view of head drawn as a dissected object to show labral and maxillary muscles.

Aulacinae.—The head of *Aulacus* (fig. 15) possesses large tridentate mandibles (*md*) similar to those of *Gasteruption*. *Aulacus* differs from *Gasteruption* in that the labral (*lms*), stipital (*ss*(*q*)) and labial (*lbs*) sclerites are present. These sclerites, however, are not so distinct as those of Ichneumonids and Braconids.

Aulacus possesses two palp-like processes on the stipes (*st*). The outer process is interpreted as the maxillary palp (*mplp*), and the inner as the galea (*ga*). It will be recalled that the galea of *Xiphydria* is reduced to a palp-like process. A palp-like galea has been described on the stipes of many Aculeate larvae (*see* Parker, 1934; Grandi, 1935; Menozzi, 1936; Wheeler, 1943).

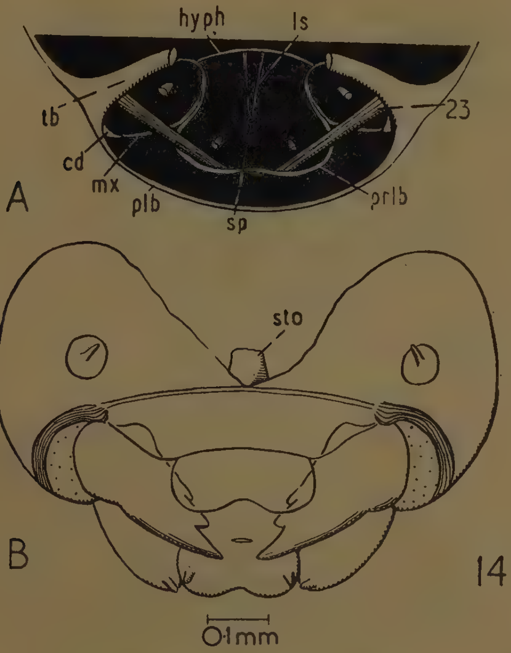

Fig. 14.—The head of *Gasteruption assectator* (L.) (Evaniidae). A. Posterior view of maxillae and labium. B. Exuviae of head of last larval instar.

Aulacus also possesses two apertures to the silk glands (*slo*). The structure of these apertures closely resembles those of some Sphecid larvae (see Giordani Soika, 1934).

The only specimen of *Aulacus* which was available for study was mounted in Faure's fluid. The ocular lines and the depressions showing the place of origin of the frontal muscles were not visible. There is no reason to doubt that these could be distinguished in a living specimen.

6. The Head of Chalcidoidea (fig. 16).

Parker (1924) has discussed the structure of Chalcidoid larvae. In this group the pleurostoma and hypostoma are only slightly defined. The various sclerites are absent. The mandibles are slender and curved, resembling those

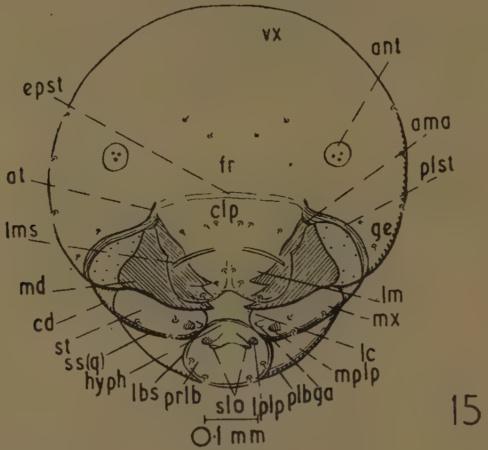
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Fig. 15.—Antero-ventral view of head of *Aulacus striatus* Jurine (Evaniidae).

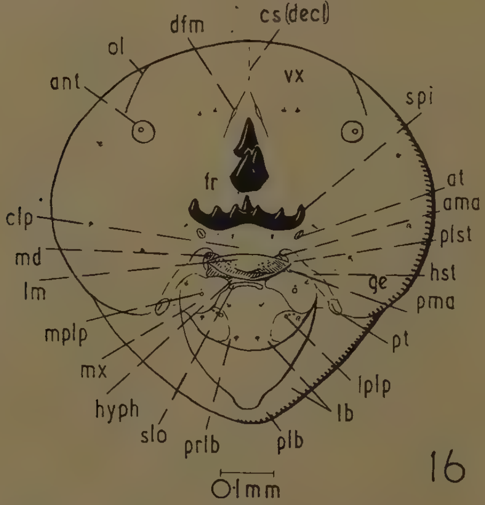
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Fig. 16.—Anterior view of head of *Stenomalus liparae* (Giraud). (Chalcidoidea).

of many Braconid larvae. The labium and maxillae are not differentiated. The prominent spines (*spi*) on the head of *Stenomalus* are specialized structures and not a characteristic of Chalcidoids.

7. THE HEAD OF CYNIPOIDEA (fig. 17).

The pleurostoma and hypostoma are defined but the epistoma is not distinct. The labial sclerite is present. The mandibles of *Rhodites* are similar in form to those of *Gasteruption* and *Aulacus*. Keilin and de la Baume Pluvinel (1913) figure the mandible of an entomophagous Cynipoid, *Eucoila keilini* Kieffer, and this is slender and curved, resembling the mandibles of many Braconids.

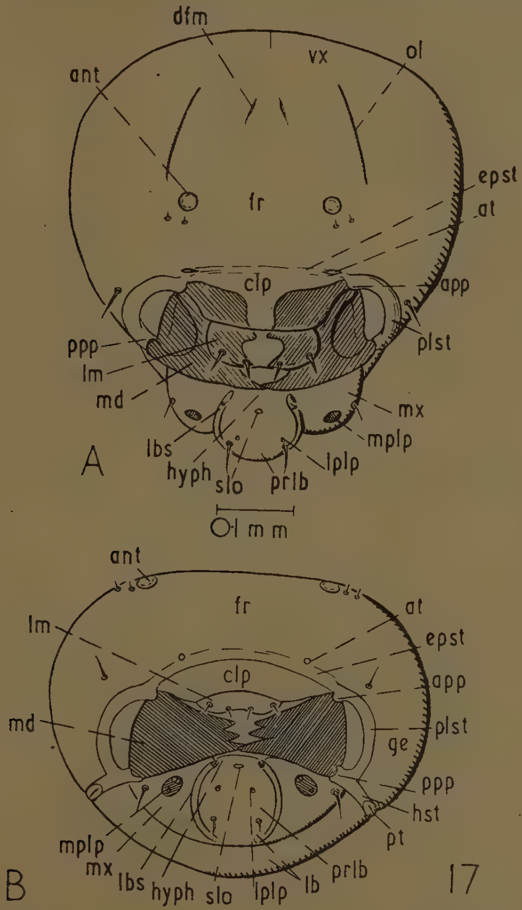
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FIG. 17.—The head of *Rhodites rosae* (L.) (Cynipoidea). A. Anterior view. B. Anteroventral view.

Roth (1949) has discussed some aspects of the morphology of the Cynipoid head.

8. The Head of Aculeata.

There are numerous papers which deal with the external structure of Aculeate larvae, but the only studies which relate skeleton to musculature are those of Nelson (1924) on *Apis*, Parker (1943) on *Polistes*, Athias-Henriot (1947) on some Formicidae and Stärcke (1949) on *Myrmica*. In no case is the description of the muscles or the attempt to state muscle homologies adequate.

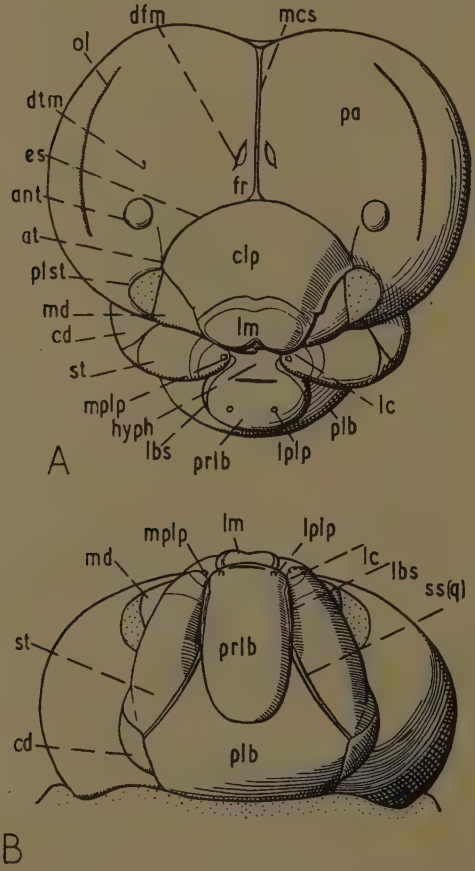
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Fig. 18.—The head of *Bombus* sp. (Apidae). A. Anterior view. B. Ventral view.

It was therefore necessary to make skeleto-muscular studies of the heads of two Aculeates.

i. The Head of the Spheciformia.

The type chosen here was *Bombus* sp. (figs. 18–21).

The only feature calling for comment is that the epistomal sulcus (fig.

18A, *es*) is connected with the postoccipital sulcus by a mid-cranial sulcus (*mcs*). At ecdysis the cranium splits down the mid-cranial sulcus (fig. 21A) and along the edge of the epistomal sulcus.

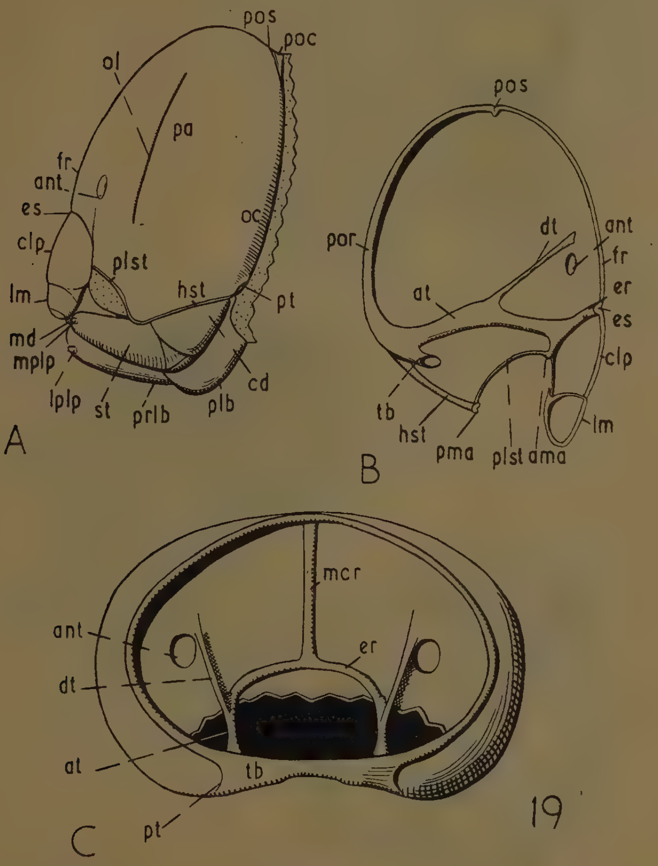
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FIG. 19.—The head of *Bombus* sp. (Apidae). A. Lateral view. B. Lateral view of left half of head capsule. C. Posterior view of cranium.

ii. The Head of Vespiformia.

The type chosen here was *Vespula sylvestris* (Scopoli) (figs. 22–24).

The only feature calling for comment is that the galea (*ga*) is present on the maxilla.

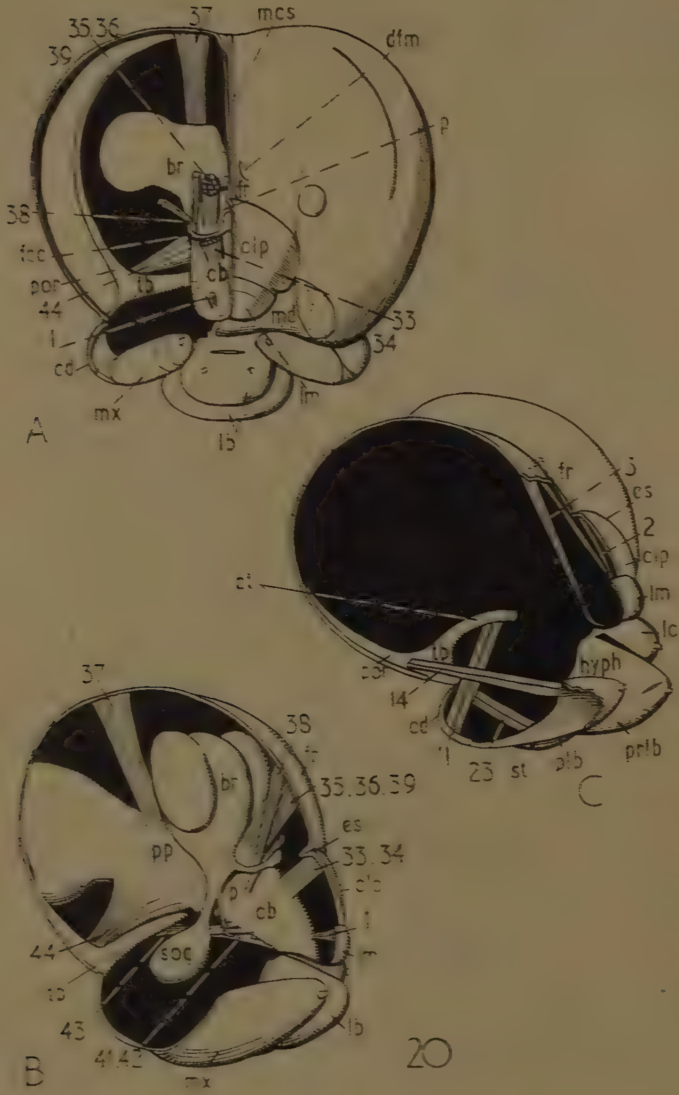
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FIG. 20.—The head of *Bombus* sp. (Apidae). A. Anterior view of dissection showing muscles of alimentary canal. B. Lateral view of dissection showing muscles of alimentary canal. C. Antero-lateral view of dissection showing labral, maxillary and labial muscles.

9. INTERRELATIONSHIPS WITHIN THE APOCRITA INDICATED BY LARVAL HEAD STRUCTURE.

There are two general types of larval head in Ichneumonoids. One type is that of Ichneumonids and Braconids which has prominent sclerotic bands (e.g., stipital and labial) and small mandibles. The other is that of Evaniidae, in which there are no prominent sclerotic bands and the mandibles are large. Crosskey (1951) has studied the morphology and taxonomy of the adult Evaniidae. He recommends that the Evaniidae be removed from the Ichneumonoidea and raised to a super-family rank.

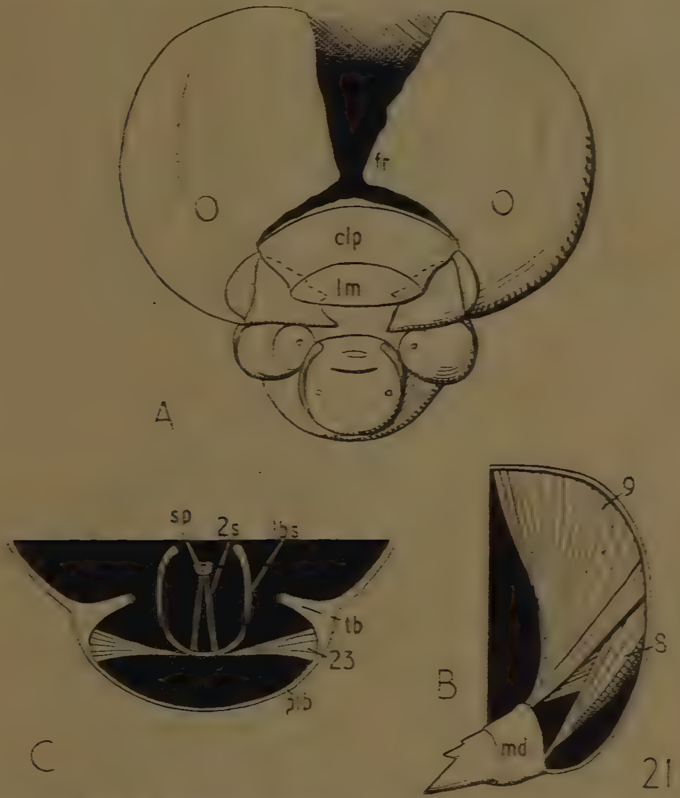

FIG. 21.—The head of *Bombus* sp. (Apidae). A. Anterior view of head exuviae of last larval instar. B. Anterior view of mandible and mandibular muscles. C. Posterior view of labium and labial muscles.

There are many intergrades between these two types of larval head. For example, *Agriotypus* possesses the usual sclerotic bands but the mandibles are large. The mandibles of *Agriotypus*, however, possess small teeth, as do the mandibles of many Ichneumonids and Braconids.

The head of Aculeates resembles that of Evaniids rather than that of Ichneumonids and Braconids. It is significant that *Aulacus* possesses two structures which were thought to be confined to some Aculeates. They are the galea on the maxilla and the two apertures to the salivary glands.

There is little variation in the fundamental structure of the larval head within the Apocrita.

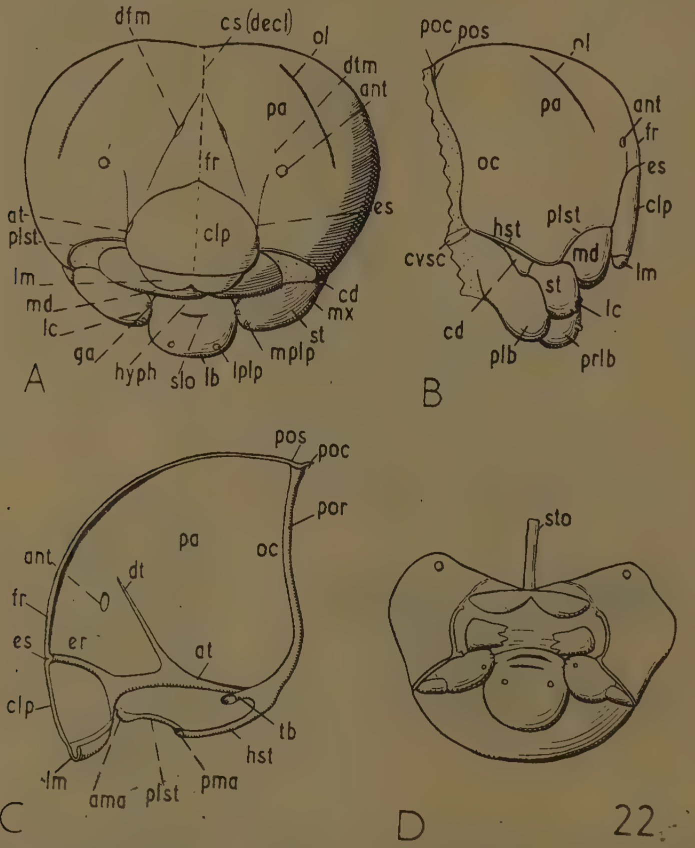
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FIG. 22.—The head of *Vespula sylvestris* (Scopoli) (Vespidae). A. Anterior view. B. Lateral view. C. Lateral view of right half of head capsule. D. Antero-ventral view of head exuviae of last larval instar.

10. METHODS AND MATERIAL.

The heads of *Sirex*, *Xiphydria*, *Gasteruption*, *Vespula* and *Bombus* were studied by the dissection of alcohol-fixed material.

Heads of *Xorides* were fixed in Carnoy and double embedded by the Peterfi method in paraffin wax of 54° C. m.p. Longitudinal and transverse sections

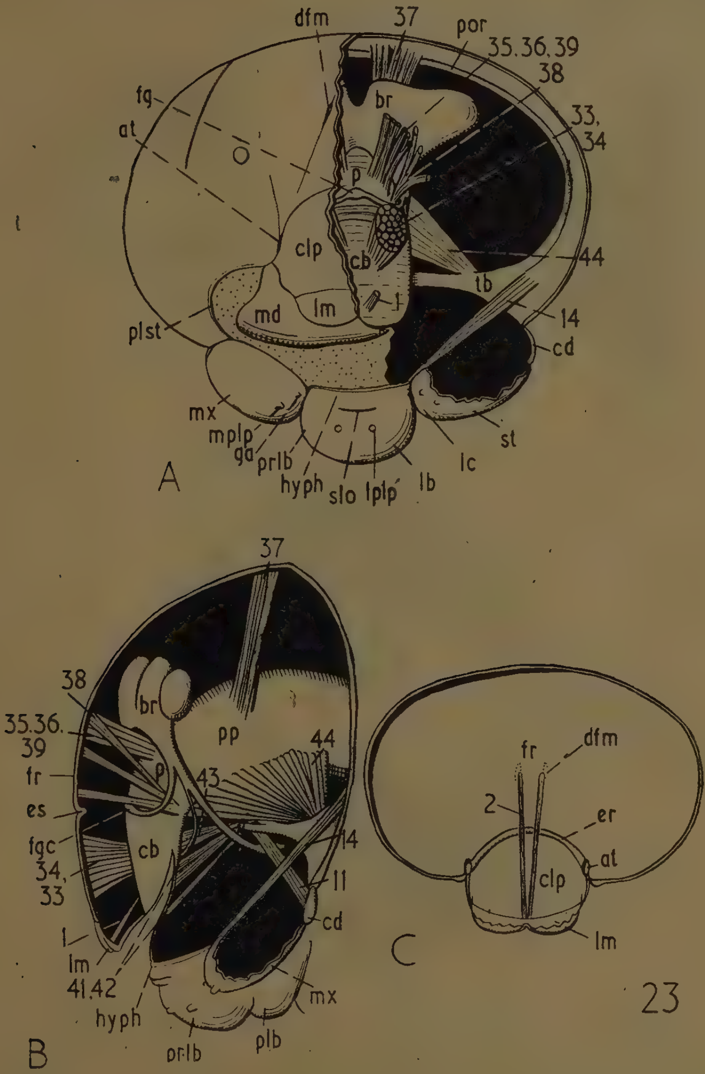
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FIG. 23.—The head of *Vespula sylvestris* (Scopoli) (Vespidae). A. Anterior view of dissection showing muscles of alimentary canal. B. Lateral view of dissection showing muscles of alimentary canal and maxilla. C. Posterior view of anterior half of cranium showing labral muscles.

were cut at 13μ. The sections were stained with Erlich's haematoxylin and counter-stained with eosin. Graphic reconstructions were made from the serial sections by the method described by Pantin (1946 : 50–51).

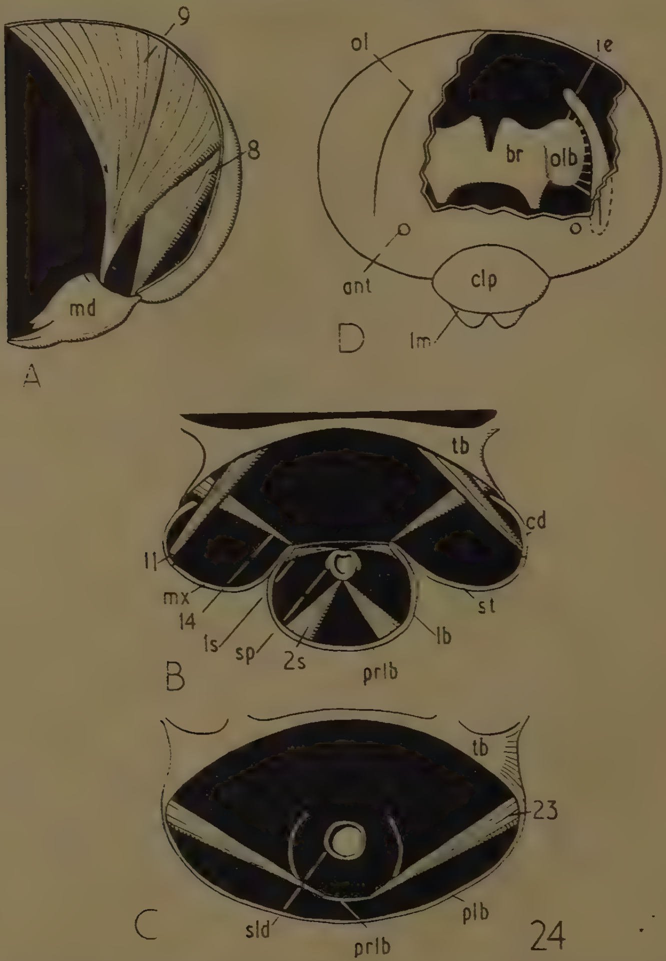

Fig. 24.—The head of *Vespula sylvestris* (Scopoli) (Vespidae). A. Anterior view of mandible and mandibular muscles. B. Posterior view of maxillae and prelabium showing maxillary and labial muscles. C. Posterior view of labium showing labial muscles. D. Antero-dorsal view of cranium showing ocular lines in association with the developing imaginal eyes.

Polarized light was used in the study of muscles.

Larvae of *Xorides* were collected in the New Forest as ectoparasites of *Rhagium bifasciatum* F.

11. ACKNOWLEDGMENTS.

This work was carried out under the supervision of Professor G. C. Varley, to whom I am indebted for much kind help.

Larvae of *Sirex*, *Xiphydria* and *Aulacus* were provided through the kindness of Dr. R. N. Chrystal, and larvae of *Gasteruption* and *Agriotypus* through the kindness of Professor Varley. Mr. H. Whitehead also assisted by providing material of *Agriotypus*.

Larvae of *Vespula* and *Bombus* were available as preserved material in the Hope Department of Entomology.

I am grateful to Dr. J. R. Baker, who directed me on certain points of histological technique, and to Mr. R. E. Snodgrass, Dr. B. M. Hobby and Dr. O. W. Richards, who have given much valuable advice. I also wish to thank Dr. F. van Emden, who identified the specimen of *Rhagium*.

12. LIST OF HEAD MUSCLES.

i. Larvae of *Sirex* and *Xiphydria*.

Head muscles of *Sirex* (omitting those of maxilla) :—

1. Compressors of the labrum. (α of Parker, 1934.)
2. Anterior retractor of labrum (absent in *Sirex*, present in *Xiphydria*). (1 of Parker.)
3. Posterior retractor of labrum. (2 of Parker.)
4. Levator of antenna.
5. Depressor of antenna. (4 and 5 are 10 of Parker.)
8. Abductor of mandible. (11 of Parker.)
9. Adductor of mandible. (12 of Parker.)
23. Posterior or ventral retractor of prementum. (26 of Parker.)
24. Anterior or dorsal retractor of prementum. (28 of Parker.)
33, 34. Anterior dilators of cibarium and buccal cavity. (3 of Parker.)
35, 36, 39. Anterior dilators of the pharynx or precerebral pharyngeal muscles. (These appear to be 4, 5 and 6 of Parker. His description and figures are not clear.)
37. Dorsal dilator of posterior pharynx. (8 of Parker.)
38. Dorsal hypopharyngeal muscle. This consists of two parts, one having origin on the frons and the other on the vertical part of the epistomal ridge. Note that this latter part of muscle 38 has origin outside the cleavage lines.
41. Ventral dilator of buccal cavity and cibarium.
43. Ventral dilator of pharynx. (7 of Parker ?)
44. Ventral dilator of postpharynx.
1*s*. Dorsal (hypopharyngeal) muscles of salivarium.
rst. Median muscles of labium.
a. A pair of muscles extends from the anterior tentorial arms to the vertex. Functions and homologies are not known. Parker (1934) describes them in *Pseudoclavellaria*. (9 of Parker.)
b. A pair of muscles has origin on the dorso-lateral aspects of the post-occipital ridge and insertion on the posterior ends of the basal sclerites of the hypopharynx. It is suggested that these muscles represent the retractors of the hypopharynx (32) of Orthopteroids. (27 of Parker.)

The maxillary muscles of larval *Xiphydria*. (The maxilla of *Xiphydria* was selected for study since the sclerites are better developed than those of *Sirex*) :—

10. Promotor of cardo. (19 of Parker.)
11. Adductors of cardo. (13 of Parker.)
12. Proximal adductor of stipes.
13*a*. First distal adductor of stipes (origin on anterior tentorial arm).
13*b*. Second distal adductor of stipes (origin on tentorial bar). (Muscles 12–13*b* are numbered 14–17 by Parker.)
14. Cranial flexor of lacinia. (20 of Parker.)
15. Stipital flexor of lacinia. (18 of Parker.)
17. Levator of maxillary palp.
18. Depressor of maxillary palp. (17 and 18 are 21 and 22 of Parker.)

ii. Larvae of Apocrita.

1. Compressors of the labrum.
2. Anterior retractors of the labrum.
3. Posterior retractors of the labrum. (Absent in *Vespula*.)
8. Abductor of the mandible.
9. Adductor of the mandible.
11. Adductor of cardo.
12, 13. Proximal and distal adductors of stipes. These may be present in *Xorides* sp. (Ich.).
14. Cranial flexor of lacinia.
23. Posterior or ventral retractor of prementum.
33, 34. Anterior dilators of cibarium and buccal cavity.
35, 36, 39. Anterior dilators of pharynx or precerebral pharyngeal muscles.
37. Dorsal dilator of posterior pharynx.
38. Dorsal hypopharyngeal muscle. In *Xorides* this has two points of origin. The main muscle strand has origin with 35, 36, 39 and the labral retractors. A slender strand has origin on the cranial walls slightly mesad of the antennae.

In *Gasteruption* only the main strand is present.

In *Bombus* the two strands are present. The main strand has origin with the remaining frontal muscles. The lateral strand has origin mesad of the antennae on a cranial sulcus connected with the epistomal sulcus.

In *Vespula* muscle 38 consists of three strands. The two median have origin with the remaining frontal muscles. The lateral has origin as in *Bombus*.

41, 42. Ventral dilator of cibarium and buccal cavity.
43. Ventral dilator of pharynx.
44. Ventral dilator of postpharynx.

The ventral dilators of the stomodaeum (41–44) can only be roughly homologized. They have, however, little diagnostic value in morphology.

1*s*. Dorsal (hypopharyngeal) muscles of the silk press. (Absent in *Bombus*.)
2*s*. Ventral (labial) muscles of the silk press. (Absent in *Gasteruption*.)

13. List of Abbreviations Used on the Figures.

al	articular line.
am	articular membrane.
ama	anterior mandibular articulation.
ant	antenna.
ant sk	antennal socket.
app	anterior pleurostomal process.
at	anterior tentorial pit and arm.
atr	atrium of spiracle.
bc	buccal cavity.
bl	blade of mandible.
br	brain.
bsh	basal sclerite of hypopharynx.
ca	closing apparatus of spiracle.
cb	cibarium.
cc	circumoesophageal connectives.
cd	cardo.
ch	hooks on caudal segment of *Agriotypus*.
clp	clypeus.
cs (*decl*)	coronal stem of dorsal ecdysal cleavage line.
cvsc	cervical sclerite.
cvx	cervix.
dfm	depressions in cranial wall at place of origin of frontal muscles.
dt	dorsal arm of tentorium.
dtm	dorsal tentorial mark.
e	eye.
elm	epipharyngeal surface of labrum.
epst	epistoma.
er	epistomal ridge.
es	epistomal sulcus.
fa	frontal arms of dorsal ecdysial cleavage line.
f-c a	fronto-clypeal apotome.
fg	frontal ganglion.
fgc	frontal ganglion connectives.
fm	food meatus.
for	foramen magnum.
fr	frons.
ga	galea.
ge	gena.
gl	glossa.
hls	horn-like sclerotizations on dorsum of head of *Agriotypus*.
hr	hypostomal ridge.
hsp	sclerotic spur of hypostoma.
hst	hypostoma.
hyph	hypopharynx.
lb	labium.
lc	lacinia.
lbs	labial sclerite.
lm	labrum.
lms	labral sclerite.
lplp	labial palp.
mcr	ridge of mid-cranial sulcus of *Bombus*.
mcs	mid-cranial sulcus of *Bombus*.
md	mandible.
mplp	maxillary palp.
mth	mouth.
mx	maxilla.
oc	occipital region of cranium.
ocr	occipital ridge.
ocs	occipital sulcus.
ol	ocular line.
olb	optic lobe of brain.
p	pharynx.
pa	parietal region of cranium.
pge	postgena.
plb	postlabium.
plst	pleurostoma.
pma	posterior mandibular articulation.
pmt	postmentum.
poc	postocciput.
por	postoccipital ridge.
pos	postoccipital sulcus.
pp	postpharynx.
ppp	posterior pleurostomal process.
pr	pleurostomal ridge.
prlb	prelabium.
pt	posterior tentorial pit.
ry	ridge of sulcus *sy*.
sh	suspensorium of hypopharynx.
sld	salivary duct or silk duct.
slo	salivary orifice or orifice of silk press.
sog	suboesophageal ganglion.
sp	silk press.

spi	spines on frontal region of *Stenomalus*.
ss (*q*)	stipital sclerite.
st	stipes.
sto	stomodaeum.
sx	sulcus of cardo.
sy	sulcus which extends from the postoccipital sulcus over the occipital and parietal cranial areas.
t	teeth of mandible.
tb	tentorial bar.
vx	vertex.

14. APPENDIX.

A Classification of the Larvae of some Families of the Hymenoptera Parasitica.

On the basis of the foregoing morphological study it is possible to revise and extend the present classification of the larvae of the Hymenoptera Parasitica.

The following key has been adapted from Thompson (1930) and Beirne (1941). The characters listed are, unless otherwise stated, those of final instar larvae. The features of the larvae of the Hymenoptera Apocrita are first listed for contrast with those of the Diptera Cyclorrhapha.

Larvae legless; cylindrical in form, though sometimes with a spherical or conical tail; three thoracic and ten abdominal segments in most forms, though various exceptions exist; mouth parts consisting of a pair of opposable mandibles, each articulating with a pleurostoma at the side of the mouth opening; maxillary and labial palpi sometimes present or represented by definitely circumscribed sensorial areas, but sometimes absent; with a definite head capsule, often pigmented, often large, not retractile, bearing microscopic sensilla and setae; pharyngeal wall without a heavily sclerotized skeleton; tracheal system apneustic, metapneustic, or peripneustic, with spiracles approximately equal in size and similar in form; cuticle of body unpigmented except in early stages of some Chalcidoids (Perilampidae, Eucharidae); setae often present but usually feebly pigmented; bands of highly pigmented spines usually not present; four or five larval stages; parasitic forms ectophagous or endophagous; endophagous forms usually lying free within body cavity without contracting a respiratory relation with the external air . . . . **Hymenoptera Apocrita.**

1 (10) Maxillary and labial appendages present or sensilla arranged in definitely circumscribed maxillary and labial areas, at least in later stages of development; cocoons usually formed.
2 (3) Sclerotic spur of hypostoma absent; mandibles large and tridentate or bidentate . . . . **Evanidae** and **Hymenoptera Aculeata.**
3 (2) Sclerotic spur of hypostoma present at least in primitive forms; mandibles slender.[4]
4 (5) Mandible large; caudal hooks present on second and third instar larvae . . . . **Agriotypidae.**
5 (4) Mandible slender; caudal hooks absent.
6 (7) Mandibles and head sclerites only visible with staining; accessory longitudinal tracheal commissure not present **Ichneumonidae** subfamily **Collyriinae.**

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[4] Except *Agriotypus*

7 (6) Mandibles or head sclerites or both are visible in final instar without staining.

8 (9) Accessory longitudinal tracheal commissure present in thorax; early instar larvae of endophagous forms often caudate; mandibles usually simple in endoparasites; mandibles usually toothed in ectoparasites, and teeth are present on lower edge of mandible as well as upper in some species; a labral sclerite present in ectoparasites (except *Adelognathus*); sclerotic spur of hypostoma usually present and always fused to hypostoma, rarely also lightly fused to stipital sclerite; prelabial sclerite sometimes present; usually solitary or feebly gregarious . . . **Ichneumonidae.**
(*See* Beirne (1941) for further treatment.)

9 (8) Accessory longitudinal tracheal commissure of thorax not present; early-instar larvae of endophagous forms often vesiculate; mandibles of endoparasites simple or toothed; mandibles toothed in ectoparasites, but teeth never present on lower edge of mandible; a labral sclerite never present in final instar[5]; sclerotic spur of hypostoma often present and may be fused to stipital sclerite only; prelabial sclerite never present; either gregarious, or solitary **Braconidae.**

10 (1) Maxillary and labial areas not differentiated, the sensilla below the mouth opening not grouped on definitely circumscribed regions; mandibles usually simple; pleurostoma and hypostoma lightly sclerotized; no accessory longitudinal tracheal commissure in the thorax; apneustic, metapneustic, or peripneustic, spiracles variable in number and arrangement; endophagous forms sometimes with a tail; body cuticle usually colourless, but highly pigmented in the first instar larvae of the Eucharidae and Perilampidae; ectophagous or endophagous; gregarious or solitary; cocoons[6] seldom formed . . . . **Chalcidoidea.**
(*See* Parker (1924) for further treatment.)

With our present state of knowledge of the larvae of the Aculeata it is not possible to differentiate the Evaniidae from the Aculeata. Giordani Soika's (1934) key to the families of the Apocrita is very incomplete.

The subfamilies of the Evaniidae may be grouped as follows:

Galea present; double aperture to silk glands . . . . **Aulacinae.**
Galea absent; single aperture to silk glands
Gasteruptioninae and **Evaniinae** (Genieys, 1924).

It was not possible to attempt to differentiate the Evaniinae and Gasteruptioninae since a specimen of the Evaniinae was not available for study.

There is no one character which distinguishes Braconids from Ichneumonids. For example, a vesiculate first instar is found in many Braconids (mainly Microgastrinae). This type is also found in some Ichneumonids (see Clausen, 1940).

15. SUMMARY.

i. The basic Pterygote head is hypognathous. The cranium is well sclerotized. Compound eyes are present. The antennae are setaceous. The mouth parts are of the biting type.

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[5] Except *Colastes* (Beirne, 1946).

[6] The question of cocoon formation in endoparasitic Chalcidoids is unsettled (*see* Flanders. 1938).

ii. The heads of Siricidae and Xiphydriidae are examined as types of the Symphyta resembling the parasitic forms in structure. In these families the head is partially prognathous. The cranium is weakly sclerotized except for certain areas (pleurostomal, hypostomal) surrounding the mouth parts. The eyes and antennae are reduced. The maxillae and labium are reduced and fused with the hypopharynx to form an under-lip complex.

iii. The head of the larvae of the Apocrita does not vary very much in fundamental structure. The head is prognathous. Sclerotization is further reduced from the condition in *Sirex* and *Xiphydria*. However, the pleurostoma and hypostoma are usually distinct. The antennae, maxillae and labium are further reduced. Sclerotic bands (stipital, labial, etc.) are often present in association with the maxillae and labium.

Two types of head can be recognized in Ichneumonoids. In the Ichneumonidae, Braconidae and Agriotypidae the sclerotic bands in association with the maxillae and labium are prominent. The mandibles are small. In the Evaniidae the sclerotic bands are not prominent and the mandibles are large.

The head of Aculeates resembles that of Evaniids rather than the Ichneumonid-Braconid type.

iv. A classification of the larvae of some families of the Hymenoptera Parasitica is given.

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PART 2.—A CLASSIFICATION OF THE FINAL INSTAR LARVAE OF THE BRACONIDAE.

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A. INTRODUCTION AND ACKNOWLEDGMENTS.

Classification schemes which are based on larval characters are useful in that they assist workers to identify material in the larval stage. Such schemes are also of great value to the taxonomist. Relationships shown by larval characters clarify the preceding classifications based on adult characters.

Van Emden (1929) and De Beer (1940) have considered the relationships between classifications built upon adult characters and those built upon larval characters.

I am indebted to Professor G. C. Varley, who supervised this work. Mr. G. E. J. Nixon's advice on the classification and relationships of adult Braconids has been most helpful. I wish to thank Mr. J. F. Perkins, of the British Museum (Natural History), for permission to study material. Professor Varley kindly made available to me his collection of Ichneumonoid larvae. Dr. A. M. Easton, Mr. R. L. E. Ford and Mr. A. W. Stelfox have also kindly supplied material.

B. TERMINOLOGY.

Much of the classification listed is based on the structure of the head. Reference should be made to the first part of this paper, especially to fig. 6, for the basis of the terminology used in the key for the parts of the head.

C. MATERIAL AND METHODS.

The following key to the final instar larvae of the Braconidae is based on the structure of the head (sclerites, mandibles and antennae), spiracles and skin. British Museum material was used whenever possible in order to ensure correct identification. Most of the material studied has been deposited at the British Museum (Natural History). The remainder has been deposited at the Hope Department of Entomology, Oxford.

The list is very incomplete because there was not very much material available. However, most of the common genera have been examined and figured.

All the heads have been drawn as flattened objects. These diagrams are therefore morphologically inaccurate, for the head has the form of a hemisphere. This is, however, a satisfactory method for taxonomic purposes since all the relevant head structures can be shown in the one diagram.

The spiracle which is figured is never taken from any particular region of the body. In Braconids there is little variation in the form of the spiracle over the different parts of the body. Also, the character which was found to be most useful was the distance of the atrium from the closing apparatus. The spiracle which best illustrated this character was chosen regardless of position.

Skin structure has been taken from the mid-dorsal region of the second thoracic segment. A detailed " setal map " was not thought necessary. It is sufficient to indicate the appearance of the characteristic spines and setae of the skin.

In the key the epistoma, pleurostoma, hypostoma and sclerotic bands are described as being present or absent. This means sclerotized (pigmented) or unsclerotized (unpigmented) (see Wigglesworth, 1948). There is every gradation between a sclerotized and unsclerotized condition. It is hoped that confusion on this point is avoided in the key. Skeletal parts have been called sclerotized or unsclerotized only when the relevant condition is clearly shown.

Most of the specimens were available as cast skins in the cocoons of bred material. This material was treated by making a longitudinal cut in the cocoon and removing the contents (last larval skin, meconium and pupal skin). These contents were boiled in water and the softened larval skin was then stretched out and mounted in Faure's fluid.

Fresh larvae were opened by a mid-ventral incision and gently boiled in a 5 per cent. solution of caustic potash. They were then washed in water and mounted.

D. Key to the Final Instar Larvae of the Braconidae.

1 (2) Spiracle long and funnel-shaped with no apparent division into atrium and closing apparatus ; parasites of Aphids **Aphidiinae.** 11.
2 (1) Spiracle consisting of obvious atrium and closing apparatus ; not parasites of Aphids.
3 (12) Mandibles with teeth or with bifid tip to blade.
4 (5) Epistomal arch complete ; antennae papilliform **Braconinae** (except **Rogadini**). 1.
5 (4) Epistomal arch incomplete ; antennae disc-shaped.
6 (9) Hypostomal spur reduced to a small process on hypostoma ; hypostoma well sclerotized ; that part of hypostoma posterior to hypostomal spur is many (at least ten) times the length of hypostomal spur.
7 (8) Tips of mandibles bifid[7] . . . . **Microgastrinae.** 4.
8 (7) Tips of mandibles not bifid . . . . **Macrocentrinae.** 5.
9 (6) Hypostomal spur present or absent ; hypostoma present or absent ; if part of hypostoma posterior to hypostomal spur is present, it is approximately equal in length to hypostomal spur.
10 (11) Body setae very large and approximately equal in length to blade of mandible . . . . **Sigalphinae.** 3.
11 (10) Body setae of normal size, very much smaller in length than blade of mandible ; labial sclerite quadrate in shape . . **Agathidinae.** 6.
12 (3) Mandibles without teeth and tip of blade never bifid.

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[7] Except *Apanteles triangulator* (Wesm.), and *A. inclusus* (Ratz.).

13 (14) Mandibles with tips meeting or crossing in median line ; parasites of Lepidopterous larvae ; pupate within host **Braconinae**, tribe **Rogadini**. 2.

14 (13) Mandibles with tips not meeting or crossing in medial line[8] ; if parasites of Lepidopterous larvae (some Euphorinae), they do not pupate within host.

15 (16) Mandibles small in proportion to size of head ; hypostomal spur fused to stipital sclerite only and never fused to hypostoma ; spiracles with closing apparatus close to atrium ; parasites of Coleoptera, Hemiptera and Lepidoptera **Blacinae**. 7, and **Euphorinae**. 8.

16 (15) Mandibles not small in proportion to size of head ; hypostomal spur, if present, extending from hypostoma to stipital sclerite ; spiracles with closing apparatus not close to atrium ; parasites of Diptera.

17 (18) Labial sclerite complete ventrally . . . . **Opiinae**. 9.

18 (17) Labial sclerite, if present, is incomplete ventrally[9] . . . **Alysiinae**. 10.

In the following notes on the various groups of Braconids there is given a list of the species which have been examined. A list is also given of those descriptions in the literature which are thought sufficiently detailed to aid workers in identifying material.

The classification and nomenclature of Kloet and Hincks (1945) is followed whenever possible. However, it was found necessary to separate the tribes of the subfamily Helconinae (Polymorphini). These tribes are given subfamily ranking, e.g., Blacinae, Opiinae. Other alterations with regard to the placing of genera are noted below.

In a number of cases the antennae are recorded as not being visible. This does not imply that the antennae are thought to be absent. When the antenna has the form of a flattened disc, it is often impossible to distinguish it in a cast skin.

1. Subfamily BRACONINAE (Vipioninae, Cyclostomini) (Fig. 25).

Tribe Braconini :—The following species have been examined : *Bracon terebella* Wesm., *B. picticornis* Wesm., *B. simulator* Szépl., *B. stabilis* Wesm., *B. marshalli* Szépl., *Coeloides abdominalis* (Zett.). The following are figured in the literature : *Atanycolus* sp. (Schimitschek, 1929), *Bracon brevicornis* Wesm. (Genieys, 1925 ; Goidanich, 1931), *B. terebella* Wesm. (Salt, 1931), *B. tachardiae* Cam. (Glover, 1934), *B. triangularis* Nees (Lucchese, 1939), *Coeloides dendroctoni* Cushman (De Leon, 1934).

Tribe Exothecini :—*Oncophanes laevigatus* (Ratz.) has been examined. *Phanomeris phyllotomae* Mues. is figured by Dowden (1941) and *Colastes braconius* Hal. by Beirne (1946).

Tribe Spathiini :—*Spathius critolaus* Nixon is figured by Krishna Ayyar (1940).

Tribe Hecabolini :—*Heterospilus cephi* Rohwer is figured by Hill and Smith (1931) and *Ecphylus silesiacus* (Ratz.) by Russo (1938).

Tribe Doryctini :—*Dendroster middendorffii* (Ratz.) has been examined. *Dendroster protuberans* (Nees) is figured by Russo (1938). This author does

[8] Except *Aspilota*.

[9] Except *Dapsilarthra*.

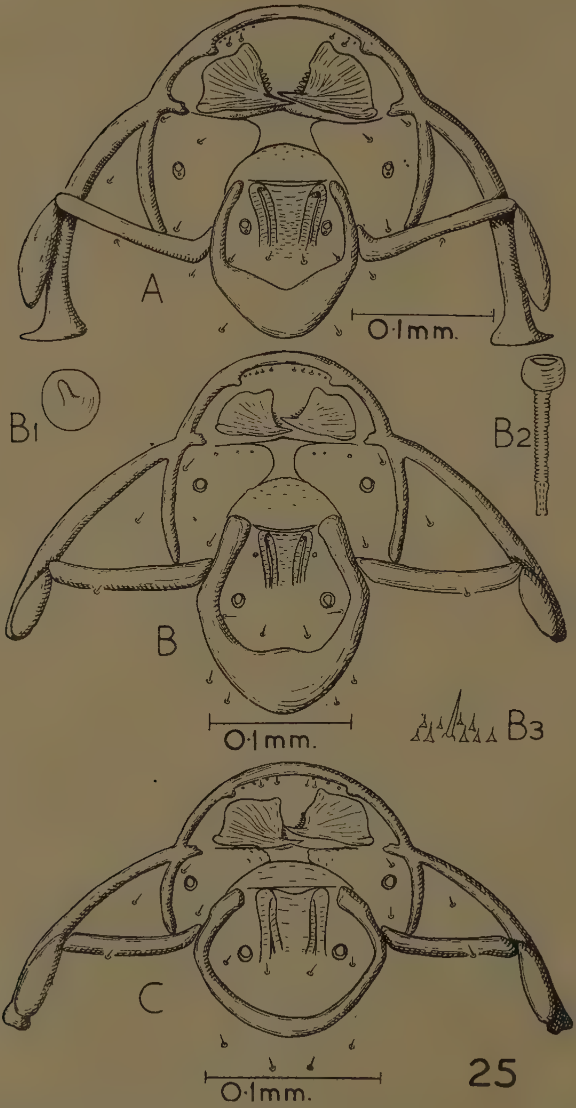

Fig. 25.—Subfamily Braconinae. A. *Bracon terebella* Wesm. (Tribe Braconini). B. *Dendroster middendorffii* (Ratz.) (Tribe Doryctini). B1, antenna. B2, spiracle. B3, skin. C. *Oncophanes laevigatus* (Ratz.) (Tribe Exothecini). The antenna, spiracle and skin are similar in these three tribes. It was therefore not necessary to figure these structures in each diagram.

not figure teeth on the mandible. Teeth are clearly visible in *D. middendorffii* and it is unlikely that *D. protuberans* differs in this respect.

Most of the genera of the tribes which are listed above are ectoparasites. (*Colastes* (Beirne, 1946) is an endoparasite). The tribes are also similar in the structure of the head, skin and spiracles. The papilliform antennae and the presence of all the head sclerites are characteristic of the group. The shape of the mandible with its quadrate base and short blade is distinctive, as is the shape of the silk press. The skin of the body always bears definite spines and setae.

Given adequate material, it might be possible to separate the tribes of the Braconinae on such characters as the number of teeth on the mandible and the structure of the palps. With regard to the latter character, however, it is significant that Rosenberg (1934) has shown that in *Ascogaster* there is individual variation in the structure of the palps.

The Braconinae possess the most generalized head structure in the Braconidae.

2. Subfamily Braconinae, tribe Rogadini (Fig. 26).

The following have been examined: *Rogas circumscriptus* Nees, *R. testaceus* (Spin.), *Petalodes unicolor* Wesm., *Spinaria spinator* Guér., *Batotheca* sp. The following are figured in the literature: *Rogas unicolor* (Wesm.) (Dowden, 1938), *R. testaceus* (Spin.) (Muzaffer Ahmad, 1944).

The epistomal arch is absent in some genera of this tribe (*Rogas*, *Petalodes*), but the remaining sclerites are always present. The head sclerites are only lightly sclerotized. The skin is relatively smooth, being covered with small conical projections.

Rogas and *Petalodes* are markedly similar. *Spinaria* and *Batotheca* are markedly similar. *Spinaria* and *Batotheca* differ from *Rogas* and *Petalodes* in that the epistomal arch is complete and the closing apparatus of the spiracle is close to the atrium.

Spinaria and *Batotheca* were studied from cast skins and the antennae were not visible.

The Rogadini differ from other members of the Braconinae in that they are endoparasites which pupate within the host. They also differ in such structural features as the non-papilliform antennae, the slender or incomplete epistomal arch and the relatively smooth skin. These differences are notable since, on the characters of the adults, the Rogadini are usually placed within the Braconinae. It is possible that the larvae of the Pambolini and Hormiini, which were not available for study and are not figured in the literature, might link the Rogadini to the other tribes of the Braconinae. On the present evidence, the larval characters of the Rogadini must be regarded as being very different from the remainder of the Braconinae.

3. Subfamily Sigalphinae (Cryptogastrini) (Fig. 27).

Tribe Sigalphini (Chelonini) :—*Chelonus* sp. was examined. The following are figured in the literature: *Ascogaster quadridentatus* Wesm. (Rosenberg, 1934; Cameron, 1938), *Chelonus annulipes* Wesm. (Vance, 1932).

Chelonus and *Ascogaster* are very similar. The characters which are distinctive of these genera are the broad blades of the mandibles, the short, broad hypostoma, the definite labial and stipital sclerites, the large number of maxillary setae behind the hypostomal spur, and the large number of prelabial setae. The hypostomal spur does not reach the stipital sclerite.

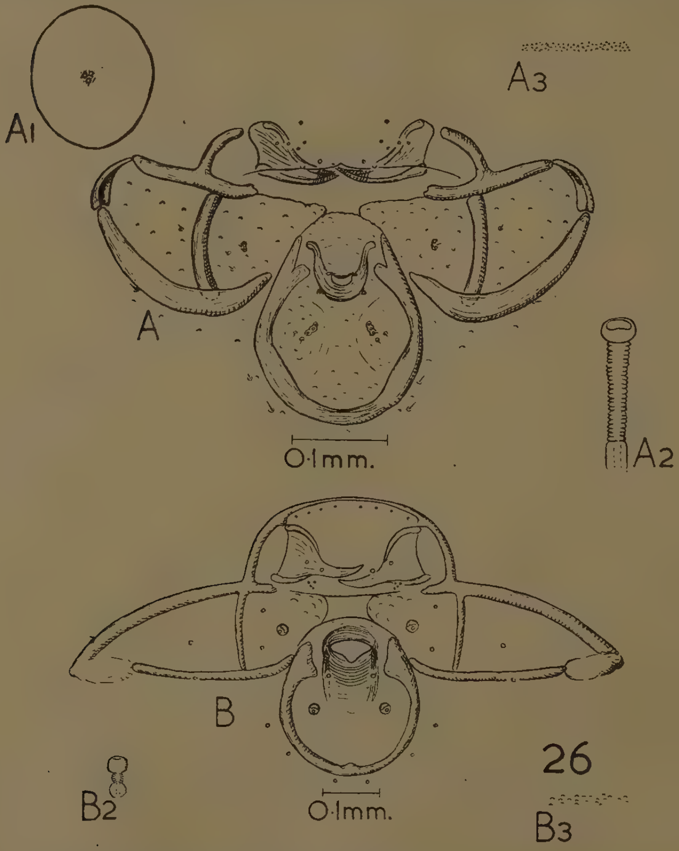

FIG. 26.—Subfamily Braconinae, Tribe Rogadini. A. *Rogas circumscriptus* Nees. A1 antenna. A2, spiracle. A3, skin. B. *Batotheca* sp. B2, spiracle. B3, skin.

Tribe Triaspidini :—*Triaspis pallipes* (Nees) was examined. *T. pallipes* is figured by Beirne (1946).

The antenna was not visible in the specimen examined. Beirne figures the antenna as an oval disc.

Beirne's figure of *Triaspis* differs from the one given in this paper in that the pleurostoma, hypostoma and hypostomal spur are shown as distinct sclerites. This difference is probably due to the fact that the diagram of the present paper was made from a cast skin whilst Beirne's diagram from a preparation of a fresh larva. In a fresh larva the pleurostoma, hypostoma and hypostomal spur are probably visible as thickenings of the cuticle. But it is doubtful that they are present as definite sclerites since these sclerites are not distinct in cast skins.

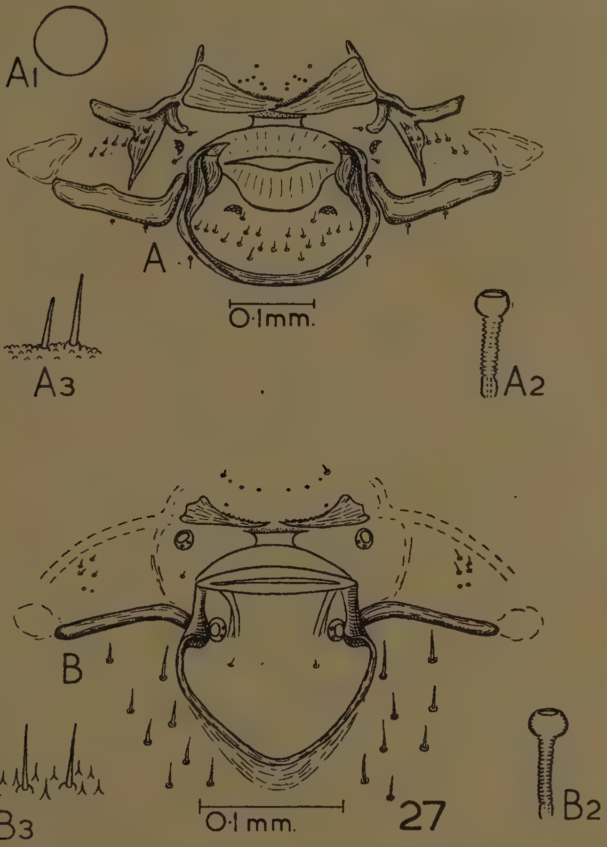

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FIG. 27.—Subfamily Sigalphinae. A. *Chelonus* sp. (Tribe Sigalphini). A1, antenna. A2, spiracle. A3, skin. B. *Triaspis pallipes* (Nees) (Tribe Triaspidini). B2, spiracle. B3, skin.

A similar condition may be seen in *Perilitus*. Here the hypostoma is visible in fresh material as a thickening of the cuticle, but this thickening is very lightly sclerotized. The hypostoma is not distinct in cast skins of *Perilitus*. It would therefore be misleading to figure the hypostoma of *Perilitus* as a distinct sclerite.

Both the Sigalphini and Triaspidini possess the distinctive giant setae on the body. However, the remaining larval characters do not indicate a close relationship.

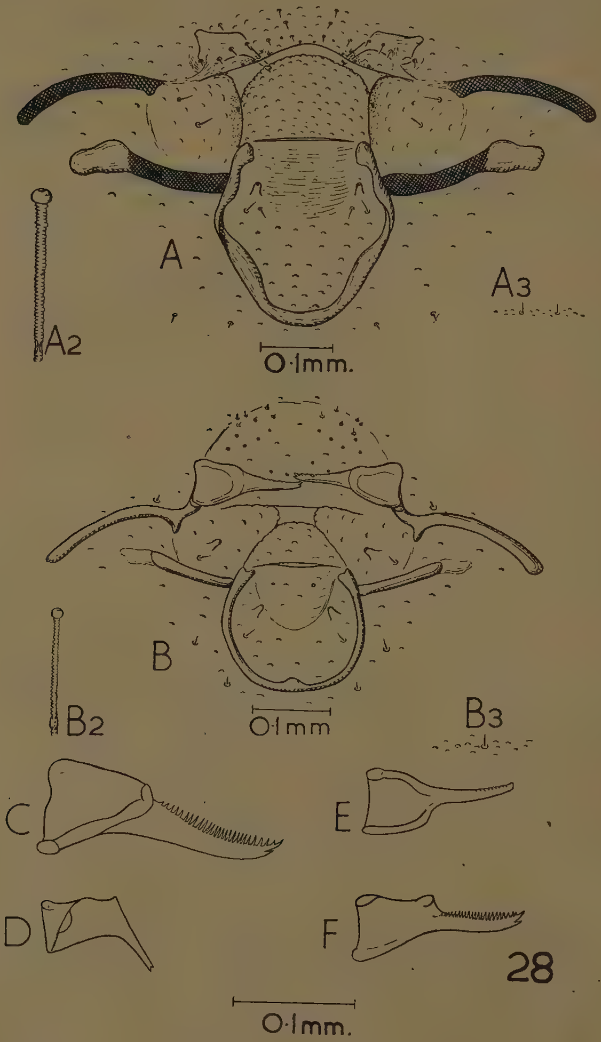


FIG. 28.—Subfamily Microgastrinae. A. *Microplitis spinolae* (Nees). A2, spiracle. A3, skin. B. *Apanteles compressiventris* Mues. B2, spiracle. B3, skin. C. Mandible of *Microgaster subcompleta* Nees. D. Mandible of *Microplitis spinolae* (Nees). E. Mandible of *Apanteles glomeratus* (L.) F. Mandible of *Apanteles lacteicolor* Vier.

4. Subfamily MICROGASTRINAE (Fig. 28).

The following have been examined: *Apanteles butalidis* Marsh., *A cajae* (Bouché), *A. carbonarius* (Wesm.), *A. compressiventris* Mues., *A. cupreus* Lyle, *A. emarginatus* (Nees), *A. fraternus* Reinh., *A. glomeratus* (L.), *A. inclusus* (Ratz.), *A. laetus* Marsh., *A. lacteicolor* Vier., *A. praepotens* (Hal.), *A. melitaearum* Wilk., *A. rubecula* Marsh., *A. sibyllarum* Wilk., *A. triangulator* (Wesm.), *Microgaster subcompleta* Nees, *Microplitis mediator* (Hal.), *M. spinolae* (Nees), *M. xanthopus* (Ruthe). The following are figured in the literature: *Apanteles congregatus* Say (Fulton, 1940), *A. fumiferanae* Vier. (Brown, 1946), *A. sesamiae* Cam. (Ullyett, 1935), *A. solitarius* (Ratz.) (Parker, 1935), *A. thompsoni* Lyle (Vance, 1931), *Microgaster polita* Marsh. (Ahlberg, 1927).

The larval characters indicate a very distinct group. The hypostoma, stipital sclerite and labial sclerite are always present. The hypostomal spur is always reduced to a small process on the hypostoma. The pleurostoma is weakly sclerotized and the epistoma is always absent.

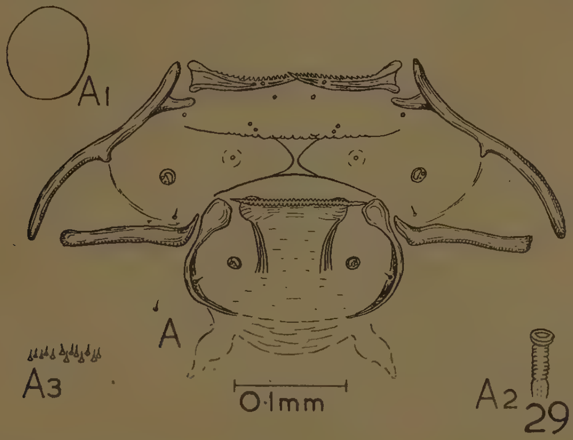


FIG. 29.—Subfamily Macrocentrinae. A. *Macrocentrus linearis* (Nees). A1, antenna. A2, spiracle. A3, skin.

The tips of the mandibles are usually bifid. In some cases this character may be difficult to see because of the position in which the mandible is mounted. There is a great deal of variation in the form of the mandible in the Microgastrinae (see figs. C–F). Within the genus *Apanteles* the mandibles of some species possess very slight teeth and the mandibles of other species have pronounced teeth.

The antenna has not been seen in any member of the Microgastrinae. Living larvae of *A. glomeratus* were examined, but a distinct antenna could not be distinguished. It is probable that there is no distinct antenna in this group. Ullyett (1935) found no signs of an antenna in *A. sesamiae*.

Setae are always present on the skin of the body. Spines are not present.

Microplitis may be distinguished from *Microgaster* and *Apanteles* as follows:

Maxillary palp is a pigmented disk . . . . **Microplitis.**
Maxillary palp is papilliform . . . . **Microgaster** and **Apanteles.**

5. Subfamily MACROCENTRINAE (Fig. 29).

Macrocentrus linearis (Nees) was examined. In this subfamily the hypostomal spur is reduced to a small process on the long hypostoma. The epistoma is absent. The stipital sclerite is present. The lateral parts of the labial sclerite are well sclerotized, but the ventral part is weakly sclerotized and has the form of a broad plate. The aperture of the silk-press is crenate. The mandible is toothed, long and slender. The skin is covered with small spines. Setae are not present.

The larval characters of *Macrocentrus* show no relationship to those of the Blacinae, Euphorinae and Opiinae.

Note: *Zele* has been considered as a member of the Agathidinae.

6. Subfamily AGATHIDINAE (Fig. 30).

The following have been examined: *Agathis* sp., *A. rufipes* (Nees), *Disophrys* sp., *Orgilus obscurator* (Nees), *Zele infumator* Lyle. The following are figured in the literature: *Agathis vulgaris* (Cress.) (Simmonds, 1947), *Orgilus obscurator* (Nees) (Thorpe, 1930).

The distinctive characters of this subfamily are the mandibles with their quadrate bases and long, slightly-curved, toothed blades and the quadrate labial sclerite. The stipital sclerite is always distinct.

Disophrys is similar to *Agathis*. In the specimen of *Disophrys* which was examined the hypostoma and hypostomal spur were more complete than is the case in the specimen of *Agathis* which is figured.

Orgilus is placed in the Agathidinae because of the shape of the mandibles and the shape of the labial sclerite. *Orgilus* possesses some adult characters which resemble those of the Agathidinae. However, on both larval and adult characters *Orgilus* is an isolated genus.

Zele is placed in the Agathidinae because of the shape of the mandibles and the length of the hypostoma and hypostomal spur. This genus is usually placed in the Macrocentrinae, although it is agreed that the adult characters of *Zele* are not very similar to those of *Macrocentrus*. The larval characters of *Zele* differ from those of *Macrocentrus* in two important points. These are the shape of the mandible and the shape and degree of sclerotization of the hypostoma and hypostomal spur. *Zele* does resemble *Macrocentrus* in that there is a lightly sclerotized ventral expansion of the labial sclerite. It is difficult to assess the importance of this last character. *Zele* is an isolated genus on both larval and adult characters.

7. Subfamily BLACINAE (Fig. 31).

Pygostolus sticticus (Fabr.) was examined. Kloet and Hincks place *Orgilus* in the tribe Blacini with *Pygostolus* and *Blacus*. The larval characters of *Orgilus* are very different from those of *Pygostolus*.

Pygostolus is a very distinct genus. The pleurostoma and the hypostoma are densely sclerotized, as are the labial and stipital sclerites. There is an abrupt break in the sclerotization of the hypostoma and also in the sclerotiza-

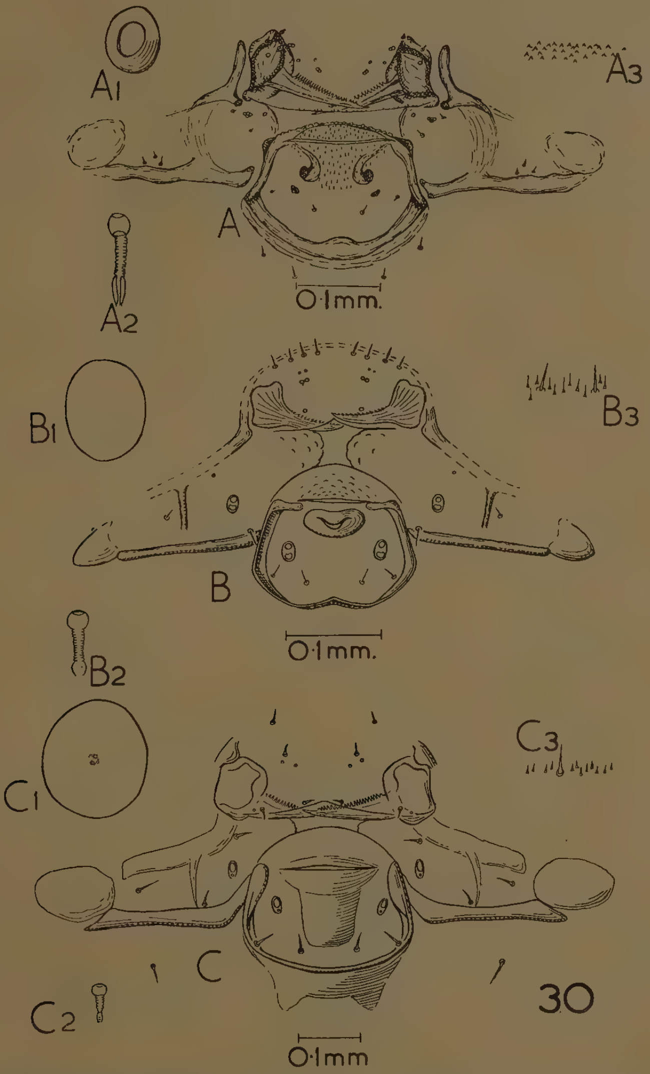
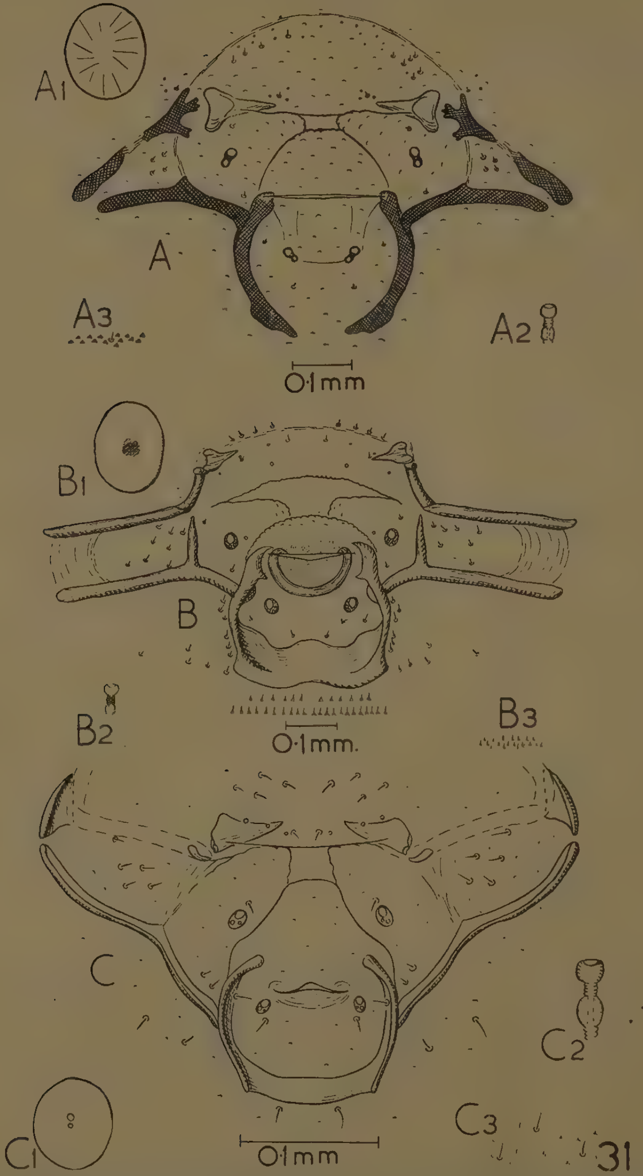


FIG. 30.—Subfamily Agathidinae. A. *Agathis* sp. A1, antenna. A2, spiracle. A3, skin. B. *Orgilus obscurator* (Nees). B1, antenna. B2, spiracle. B3, skin. C. *Zele infumator* Lyle. C1, antenna. C2, spiracle. C3, skin.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B2
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B3
C
C2
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0·1mm
C3
31

FIG. 31.—Subfamilies Blacinae and Euphorinae. A. *Pygostolus sticticus* (Fabr.) (Blacinae). A1, antenna. A2, spiracle. A3, skin. B. *Meteorus albiditarsus* (Curt.) (Euphorinae). B1, antenna. B2, spiracle. B3, skin. C. *Perilitus falciger* (Ruthe) (Euphorinae). C1, antenna. C2, spiracle. C3, skin.

tion of the labial sclerite. The skin possesses small dark spines and small setae.

It is impossible to state which of these characters might be found distinctive of the Blacinae.

8. Subfamily Euphorinae (Fig. 31).

The following have been examined: *Meteorus albiditarsus* (Curt.), *M. bimaculatus* (Wesm.), *Perilitus falciger* (Ruthe). The following are figured in the literature: *Meteorus chrysophthalmus* (Nees) (Rosenberg, 1934), *M. loxostegei* Vier. (Simmonds, 1947*a*), *Perilitus coccinellae* (Schrank) (Goidanich, 1933), *P. morimi* Ferr. (Grandi, 1931).

The Blacinae are grouped with the Euphorinae in the present key because of the small mandibles, the definite stipital sclerite and the fact that the hypostomal spur is fused only to the stipital sclerite. It is significant that, in *Perilitus* and *Pygostolus*, the hypostomal spur is reduced to a small process on the stipital sclerite. Also, in both subfamilies the closing apparatus of the spiracle is close to the atrium.

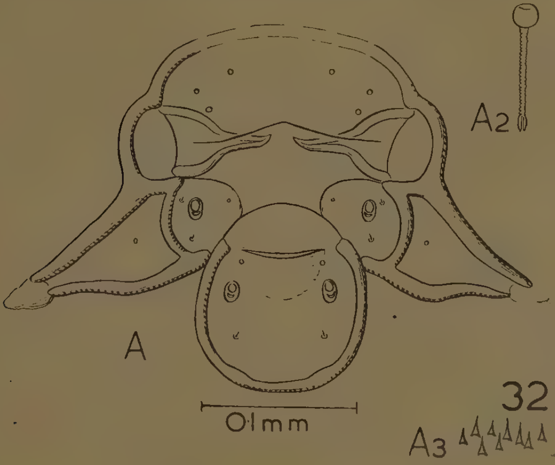


FIG. 32.—Subfamily Opiinae. A. *Opius carbonarius* (Nees). A2, spiracle. A3, skin.

It is impossible to indicate further relationships on the basis of the available material. The quadrate shape of the labial sclerite with its lateral and ventral parts meeting at right angles may be distinctive of the Euphorinae.

Perilitus may be distinguished from *Meteorus* as follows.

Hypostoma very lightly sclerotized; hypostomal spur reduced to small process on stipital sclerite . . . . **Perilitus.**
Hypostoma well sclerotized; hypostomal spur extending from stipital sclerite almost to hypostoma . . . . **Meteorus.**

9. Subfamily Opiinae (Fig. 32).

Opius carbonarius (Nees) was examined. The following are figured in the literature: *Diachasma crawfordi* Keilin and Picardo (Keilin and Picardo, 1913), *D. tryoni* Cameron (Pemberton and Willard, 1918), *Opius fletcheri* Silv. (Willard, 1920), *O. fulvicollis* Thoms. (Blunck, Bremer and Kaufmann, 1928), *O. ilicis* Nixon (Cameron, 1941).

The antennae were not visible in the species studied, but they are figured in the literature as disc-shaped areas.

The epistomal arch is very weakly sclerotized, but the remaining head sclerites are distinct. However, Cameron (1941) does not figure the stipital sclerites in *O. ilicis*. The mandibles and the maxillary and labial palps are relatively large.

The skin of the body possesses prominent spines but no setae.

10. Subfamily ALYSIINAE (Exodontes) (Fig. 33).

Tribe Alysiini :—*Alysia manducator* (Panz.) and *Aspilota vesparum* Stelfox were examined. The following are figured in the literature : *Alysia manducator* (Panz.) (Altson, 1920 ; Morgan, 1929 ; Evans, 1933), *Aphaereta minuta* (Nees) (Evans, 1933), *Aspilota vesparum* Stelfox (Evans, 1933), *Dapsilarthra gahani* de la Baume Pluvinel (de la Baume Pluvinel, 1915).

Tribe Dacnusini :—*Polemochartus liparae* (Giraud) was examined. The following are figured in the literature : *Dacnusa areolaris* Nees (Haviland, 1922), *D. gracilis* (Nees) (Wright, Geering and Ashby, 1946), *D. navicularis* (Nees) (Richello, 1928).

It is impossible to list the larval characters of the Alysiinae. The head sclerites vary from the almost complete set of *Dapsilarthra* and *Alysia* to the condition in *Polemochartus* where the only sclerotized structures of the head are the mandibles. The skin varies from the condition in *Alysia* where definite spines are present to the condition in *Aspilota* where the skin is smooth. Forms such as *Dapsilarthra* and *Alysia* resemble the Opiinae in larval characters.

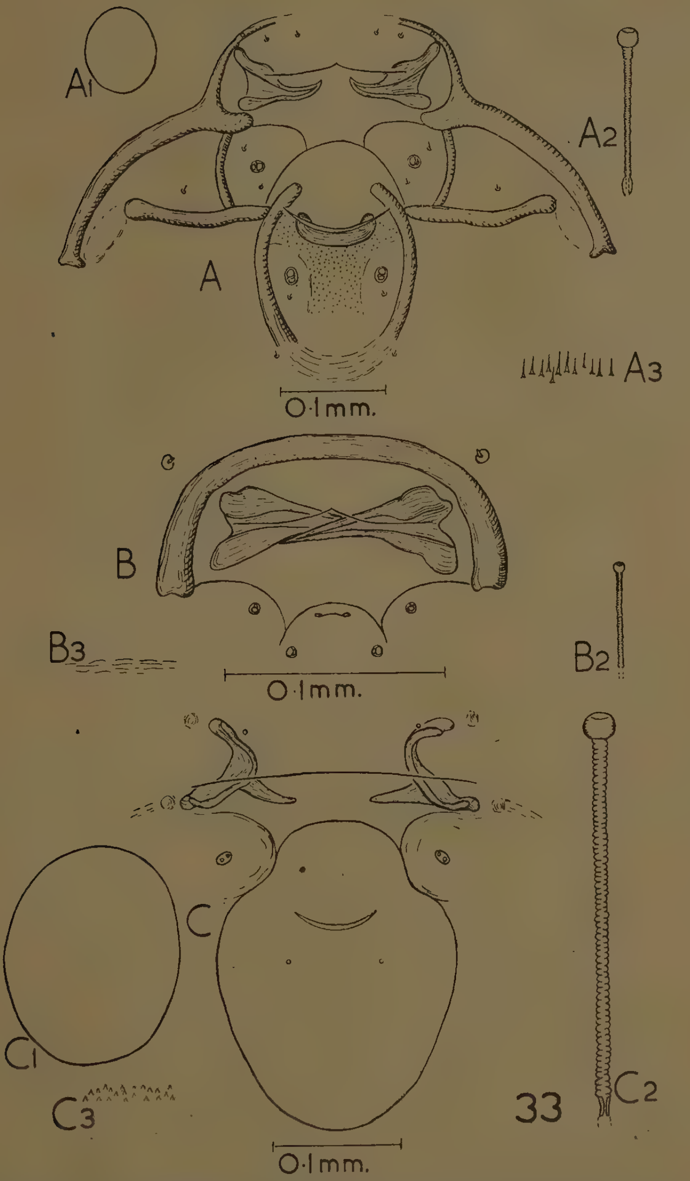
These variations are surprising since, on adult characters, the Alysiinae are a very definite group.

11. Subfamily APHIDIINAE (Fig. 34).

The following were examined : *Aphidius* sp., *A. absinthii* Marsh., *A. avenae* Hal., *A. pseudoplatini* Marsh., *A. pterocommae* Marsh., *A. ribis* Hal., *A. rosae* Hal., *A. scabiosae* Marsh., *A. urticae* Hal., *Ephedrus plagiator* (Nees), *Praon volucre* (Hal.), *Trioxys centaureae* (Hal.). The following are figured in the literature : *Aphidius* sp., (Ullyett, 1938), *Praon volucre* (Hal.) (Beirne, 1942).

The head structure is very uniform. Of the head sclerites, the epistomal arch always appears to be absent. Beirne (1942) figures the epistomal arch in *P. volucre*. In the specimens of *Praon* which were examined for this paper there is an infolding of the body wall in the epistomal region, but this infolding is not sclerotized. The hypostomal spurs appear to be absent in genera other than *Trioxys*. Beirne (1942) figures hypostomal spurs in *P. volucre*. In the specimens of *Praon* examined for this paper an infolding of the body-wall extends from each hypostoma to each stipital sclerite. These infoldings are not sclerotized. Ullyett (1938) has commented on the absence of the hypostomal spur in *Aphidius*.

The structure of the spiracles and skin is uniform in this group.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C
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FIG. 33.—Subfamily Alysiinae. A. *Alysia manducator* (Panz.) (Tribe Alysiini). A1, antenna. A2, spiracle. A3, skin. B. *Aspilota vesparum* Stelfox (Tribe Alysiini). B2, spiracle. B3, skin. C. *Polemochartus liparae* (Giraud) (Tribe Dacnusini). C1, antenna, C2, spiracle. C3, skin.

Beirne (1942*a*) has suggested that the genera of the Aphidiinae may best be separated on the form of the first instar larvae.

E. SUMMARY.

A key, based on the characters of the final instar larvae, is given for the identification of the principal subfamilies of the Braconidae.

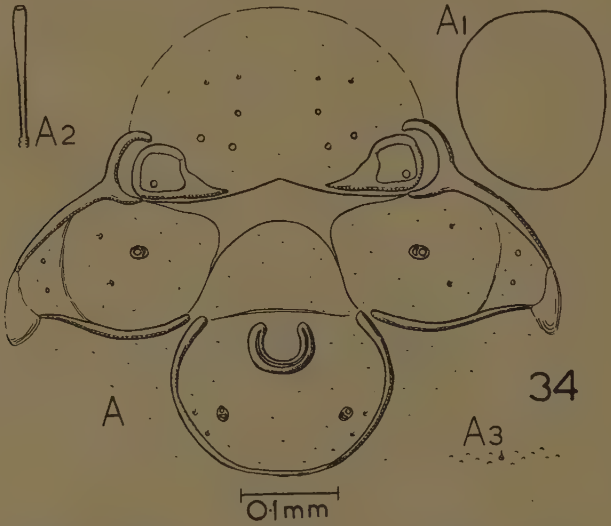

FIG. 34.—Subfamily Aphidiinae. A. *Aphidius* sp. A1, antenna. A2, spiracle. A3, skin.

The larval characters of twenty-one species have been figured and discussed. Reference is made to those descriptions in the literature which are thought sufficiently detailed to aid workers in identifying material.

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THE NEOPERLINAE OF THE ETHIOPIAN REGION (PLECOPTERA, PERLIDAE).

By H. B. N. Hynes, Ph.D., A.R.C.S.
(*Department of Zoology, University of Liverpool.*)

Manuscript received 2nd May, 1951.
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With 9 Text-figures.

This work resulted from a request from Dr. V. D. van Someren of the River Research and Development Centre, Kenya, that I identify some adult stoneflies obtained in the course of his work.

Study of the literature revealed that, with the exception of the Leuctridae of South Africa, the taxonomy of the Plecoptera of the Ethiopian region was in need of revision, as many species had been described very inadequately and often without reference to other descriptions.

I accordingly borrowed all the specimens available in various museums, and persuaded friends to collect material for me. In this way I have been able to study a considerable number of specimens from many parts of Africa, including a few relatively long series of specimens from single localities. I also borrowed some specimens from North America for comparative purposes.

Acknowledgments.

I wish to express my grateful thanks to the following persons and institutions for the loan or collection of specimens: Dr. V. D. van Someren, Mr. D. E. Kimmins of the British Museum; Dr. W. J. Hall of the Commonwealth Institute of Entomology; Miss Rosemary Lowe of the Freshwater Biological Research Station, Jinja, Uganda; Mr. E. Pinhey of the Coryndon Museum, Nairobi, Kenya; Mr. W. Crewe of the Loiasis Research Scheme, Kumba, British Cameroons; Dr. J. Aubert of the Musée Zoologique, Lausanne, Switzerland, who lent me specimens of his own and also specimens collected by Dr. G. Marlier of the Institut pour la Recherche Scientifique en Afrique Centrale, Uvira, Belgian Congo; and Dr. J. Hanson of the University of Massachusetts, U.S.A., who lent me specimens from North America.

I wish also to thank Dr. Aubert for photostat copies of three papers which I had been unable to obtain, and the Registrar and Library Staff of the Royal Entomological Society for much help in obtaining literature.

The Plecopteran Fauna of Africa.

In Algeria and Morocco the stonefly fauna appears to be closely related to that of Europe. Lestage (1925) listed several species belonging to the European genera *Perla*, *Chloroperla*, *Strobliella*, *Leuctra* and *Protonemura*. Classen (1940) listed a species of *Isogenus* from Egypt, which was originally described by Pictet (1842) in the genus *Perla*. From south of the Sahara to the Cape of

Good Hope there exist many records from scattered localities of species of Neoperlinae, which have been variously referred to the genera *Neoperla* Needham and *Ochthopetina* Enderlein. In temperate South Africa four genera of Leuctridae are found (Barnard, 1934). Therefore the only stoneflies recorded from tropical Africa are Neoperlinae. The one exception to this is a record of *Marthamea* (*Lerpa*) *beraudi* Navás, which Navás (1909) recorded from Zumbo, Mozambique, but this would appear to be an error, as a very few pages previously he described this species from Syria and made no mention of Africa.

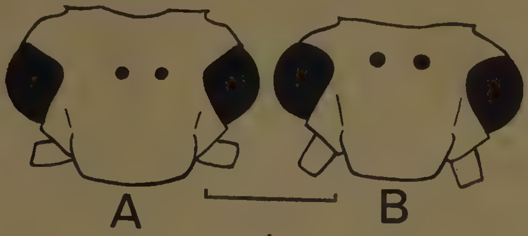
Samal (1925) has commented on the circum-equatorial distribution of the Neoperlinae, and of the genus *Neoperla* in particular, which extends from Africa through southern and eastern Asia to North America; he suggests that this supports the theory that the group arose in northern Asia or North America, at a time when these regions had a climate similar to that of the tropics of our day; it then spread with climatic change, being replaced in the north by temperate species. It is noticeable, however, that this distribution is very different from that of any group of freshwater fishes (Norman, 1947).

THE GENERA *Neoperla* NEEDHAM, 1905, AND *Ochthopetina* ENDERLEIN, 1909.

Enderlein (1909*a*) defined a genus *Ochthopetina*, which included species from Africa and East Asia. He separated this genus from *Neoperla* Needham primarily on the fact that in the hind wing of *Ochthopetina* proximal to the anastomosis the fused portion of the radial sector and median veins (Rs and M) was usually longer than its two branches (Rs and M), and was always as long as the shorter posterior branch (M). He stated that in *Neoperla*, which he regarded as an exclusively American genus, the fused portion of the radial sector and median veins (Rs and M) was at most half as long as the shorter posterior branch (M). He repeated this statement in a key in a later paper (Enderlein, 1909*b*). Klapálek (1909) considered Enderlein mistaken in erecting the new genus, and pointed out that in *Neoperla clymene* (Newman), the type-species of *Neoperla*, which is American, the venation of the hind wing is the same as that defined for *Ochthopetina*. He therefore placed several African species in the genus *Neoperla* and rejected the name *Ochthopetina*. In a later paper, however (Klapálek, 1923), he revived the name *Ochthopetina* to include two species from Java, separating them from *Neoperla* on the basis of weakly protruding eyes, and the fact that the ocelli were much closer to one another than they were to the eyes. He stated that in *Neoperla* the eyes are protruding, and the ocelli little more or only little less apart than is either from the eye. He gave a key to the African species of *Neoperla*.

These changes have resulted in much confusion. Needham (1920) placed all African species in the genus *Neoperla*, as did Lestage (1921). Chu (1928) redefined *Neoperla* in such a way that *Ochthopetina* is included in it, as is clear from his figure of the wings of *N. sinensis* Chu. Tillyard (1931) accepted the name *Ochthopetina* for the South African species, quoting the character in the hind wing given by Enderlein, and was followed in this by Barnard (1934). Tillyard also pointed out that in the hind wings of *O. transvaalensis* Enderlein the second anal vein (2A) approaches very close to the first anal vein (1A) at about a third of its length from the base, and then bends strongly away again and forks at about two-thirds of its length. He suggested that this peculiar character should be included in the generic definition if it were found to occur also in the oriental species. Finally Banks (1939) gave a key to the oriental Neoperlinae in which he used the prominence of the eyes to separate *Neoperla* and *Ochthopetina*, but he stated that in *Neoperla* the ocelli are closer together than they are in *Ochthopetina*; this is the reverse of what was stated by Klapálek (1923).

As a result of this confusion some species described from Africa have been placed in the one genus and some in the other.



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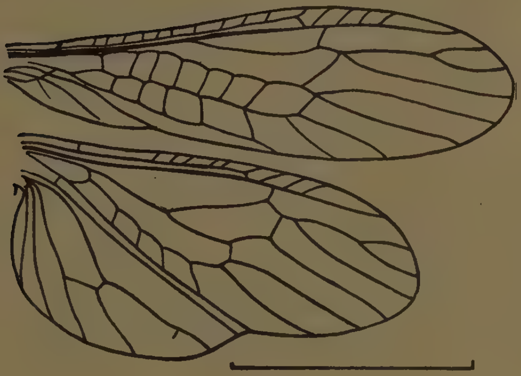

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Fig. 1.—Dorsal views of heads. A. Male *Neoperla clymene* from N. Waterboro, Me., U.S.A. B. Male Neoperline from Gura River, Kenya. The line represents 1 mm.

Fig. 2.—Right wings of male *Neoperla clymene* from Josephine Creek, Fla., U.S.A. The line represents 5 mm.

The distance apart of the ocelli is obviously not a satisfactory generic character, as Lestage (1921) has shown that it is possible to divide the described African species into three groups on the basis of whether the ocelli are further apart, nearer together or as far apart as the distance of each ocellus from the eye, and that in *N. sjöstedti* Klapálek the males and females differ in this character. Tillyard (1931) also described much variation in this character in *O. transvaalensis* where he found that the ocelli were sometimes almost touching and sometimes almost one diameter apart. Enderlein's character in the hind wing is, as stated by Klapálek (1909) and as shown below, also not valid. This leaves the prominence of the eyes and Tillyard's suggestion that the course of the second anal vein in the hind wing might prove to be a generic character. The former is a character of doubtful value and was not mentioned by Enderlein; and, as can be seen from fig. 1, it is not a character by which the American *N. clymene* can be separated from African specimens. Similarly the character in the hind wing suggested by Tillyard is not valid as, although it occurs in at least some oriental species of *Neoperla* (figures in Chu, 1928, and Kimmins, 1950), it does not occur in the species *O. aeripennis* Enderlein from Java, which Klapálek (1923) placed in his revised genus *Ochthopetina*. Also, it does occur in the American *N. clymene* (fig. 2), and is also found in some other genera of Neoperlinae, e.g., *Phanoperla* Banks and *Neoperlops* Banks, of which the hind wings are figured by Kimmins (1950).

I have examined eleven specimens of *N. clymene*, and found that the ratio of the distance from ocellus to eye to the distance apart of the ocelli varies from 1·5—2·2 : 1. In fourteen hindwings of these specimens, proximal to the anastomosis, the ratios of the lengths of the fused portion of the radial sector and median veins to the lengths of the two branches, radial sector and media, were found to vary as follows: 1 : 0·58–1·07 : 0·44–0·80. As these ratios would place the specimens in the genus *Ochthopetina*, and as this is the type-species of *Neoperla*, it seems obvious that the genus *Ochthopetina* as defined by both Enderlein and Klapálek cannot be retained. The African species should therefore be called *Neoperla* and the name *Ochthopetina* dropped.

SPECIES OF NEOPERLINAE RECORDED FROM AFRICA.

The following species of Neoperlinae have been described and recorded from various parts of Africa:

Chloroperla spio Newman (1839), SIERRA LEONE. Type redescribed by Klapálek (1923).

Perla aegyptica Pictet (1842), EGYPT.

Ochthopetina conradti Enderlein (1909*a*), CAMEROONS: Barombi. Klapálek (1923) suggested that this species is synonymous with *N. sjöstedti*.

Ochthopetina didita Enderlein (1909*a*), CAMEROONS: Barombi.

Ochthopetina camerunensis Enderlein (1909*a*), CAMEROONS: Barombi. Navás (1912) recorded from BELGIAN CONGO: Kitobola.

Ochthopetina transvaalensis Enderlein (1909*b*), TRANSVAAL: Zoutpansberg. Klapálek (1923) recorded *N. transvalensis* (*sic*) from NATAL: Mfongosi, Zululand. Tillyard (1931) and Barnard (1934) recorded from NATAL: Zululand and TRANSVAAL: Leydenberg.

Neoperla laticollis Klapálek (1909 and 1923), N. CAMEROONS: Johann Albrechtshöhe.

Neoperla dubia Klapálek (1909 and 1923), CAMEROONS: Dolodorf. Needham (1920) recorded from BELGIAN CONGO: Faradje.

Neoperla excisa Klapálek (1909 and 1923), S.W. CAMEROONS: Lolodorf, and R. NIGER: Abutschi.

Neoperla nigricauda Klapálek (1909 and 1923), N. CAMEROONS: Johann Albrechtshöhe.

Neoperla sjöstedti Klapálek (1910, 1912 and 1923), TANGANYIKA: Kilimandjaro and Ukami, and UGANDA: Ruwenzori Westseite.

Neoperla africana Klapálek (1910 and 1923), N. and S.E. CAMEROONS, FERNANDO PO and TANGANYIKA: Langenberg. He suggested that this species is synonymous with *O. camerunensis*.

Neoperla leroiana Klapálek (1911), EGYPTIAN SUDAN: Redjaf, Lado.

Ochthopetina tenera Navás (1915), ETHIOPIA: Endessa, Haut Auache.

Ochthopetina haugi Navás (1916), FRENCH CONGO: Bas Ogooué entre Lambarene et la mer. Navás (1929*a*) recorded from CAMEROONS: Mokonje Farm, Mundame, Mungo Floss, and (1931) from BELGIAN CONGO: Sankuru, Komi, Stanleyville and Ubangi, Burubu.

Ochthopetina petiolata Navás (1920), EGYPTIAN SUDAN: Roseires, Haut Nil Bleu.

Ochthopetina innexa Navás (1920), EGYPTIAN SUDAN: Roseires, Haut Nil Bleu.

Ochthopetina caudalis Navás (1920), EGYPTIAN SUDAN: Sennaar Province. Species named but not described; no description has been traced.

Neoperla lacroixi Lestage (1921), FRENCH CONGO: Fort Crampel.

Neoperla needhami Lestage (1921) (= *N .excisa* Needham *nec* Klapálek), Needham (1920) described from BELGIAN CONGO: Faradje.

Neoperla burgeoni Navás (1926), BELGIAN CONGO: Kindou, Prov. de Maniema.

Neoperla lujana Navás (1931), BELGIAN CONGO: Kivu, Buserengenye, Rutshuru.

Neoperla luluana Navás (1931), BELGIAN CONGO: Lulua, R. Luele.

Neoperla leopoldina Navás (1932), BELGIAN CONGO: Bomokandi.

Neoperla bredoana Navás (1932), BELGIAN CONGO: Waika, P. or.

Neoperla bottegoana Navás (1933), ETHIOPIA: A. Ganale Gudda, Arussi Galla.

Neoperla seyrigiana Navás (1934), KÉNYA: Meru.

Ochthopetina kunenensis Barnard (1934), SOUTH-WEST AFRICA: Erikson's Drift, Otjimbumbe, Kunene River.

Neoperla arambourgana Navás (1936), KENYA: Suam Fishing Hut, Mount Elgon.

There is perhaps some doubt if *Perla aegyptica* is really a member of the Neoperlinae as, although Pictet's description and figures are of a species closely resembling a *Neoperla*, he refers to three ocelli. Both his figures, however, show only two.

In addition to the above species Navás (1923) described a species *O. annulata* and gave the locality as " Africa ? Lib. Pinang, à la lumière." It seems possible that " Lib." refers to Liberia, and there is nothing in the description to indicate that this species differs greatly from other described African species. He also described (Navás, 1929) a species, *N. lebangina*, for which he gave no locality; this species may also be from Africa.

Many of the descriptions, particularly those of Navás, are very superficial, and almost all were based on one or very few specimens, several of which were badly damaged.

CHARACTERS USED IN THE SPECIFIC DESCRIPTIONS.

The following are the principal characters which have been described or used in keys to the African species by the various authors listed above:

(1) *Coloration.*—Particular note has been made of the shape and extent of the dark spot surrounding the ocelli, the extent of dark patches on the legs and the colour of the antennae and cerci. Klapálek (1912 and 1923) recognised that colour could be variable, and Tillyard (1931), who had only five specimens of *N. transvaalensis*, pointed out that the coloration of these was very variable.

(2) *Size.*—Almost all authors have given the sizes of their specimens either as length, length of fore wing, or wing-span. Many indicated that size is variable and that males are smaller than females. The sizes based on length of

fore wing, which would appear to be the most reliable measurement on dried and shrivelled insects, range from 7·4 to 20·4 mm.

(3) *Distance apart of ocelli and their distance from the eyes.*—Most authors have mentioned this point as a specific character, and Lestage (1921) has, as already stated, used it to divide the species into groups. Tillyard (1931), however, pointed out that it was very variable in *N. transvaalensis*, and in *N. leroiana* and *N. sjöstedi* the two sexes were described as differing in this respect.

(4) *Ratio of width to length of pronotum.*—Most species have been described as having a pronotum merely wider than long and narrower behind, but some authors have been more precise. Klapálek (1909 and 1923) has used this character in a key to the African species, despite the fact that he stated that the pronota of his specimens were not always in good shape, and also that in a paper written in 1908 (Klapálek, 1910) he referred to the same species specimens that differed in this respect. He separated his species according to whether the pronotum was more or less than three-fifths as wide as long. Enderlein (1909*a* and *b*) described the pronotum of *N. conradti* and *N. transvaalensis* as one and three-quarter times as wide as long. Navás (1920 and 1926) described the pronota of *N. innexa* and *N. burgeoni* as twice as wide as long, and of *N. petiolata* as more than twice as wide as long. Expressed therefore as a ratio of width to length, the range of the described species is $<1{\cdot}67$ to $>2{\cdot}00$. This would appear to be a very unreliable character on which to distinguish dried insects unless the differences are very marked, as pinning and drying inevitably produce distortion.

(5) *Wing venation.*—The points that have been chiefly noted about the wing venation are: the number of branches of the radial sector in the fore wing, and whether these all arise beyond the anastomosis; the number of sub-costal and costal (pterostigmal) cross-veins; and the number of procubital (M–Cu_1) and cubital (Cu_1–Cu_2) cross-veins. Klapálek (1912) has drawn attention to the fact that the number of radial sector branches may differ on the two sides of one specimen, and Tillyard (1931) stated that in *N. transvaalensis* the number and point of origin of the radial sector branches, the length of the sub-costal vein and the number of cross-veins are all very variable.

(6) *The sub-genital plate* (*eighth sternum*) *of the female.*—A sub-genital plate has been described in some species and this structure has been stated to be absent in others. In their generic descriptions Enderlein (1909*a*) and Klapálek (1909) differed as to whether a sub-genital plate is present. The following species have been described or figured as having no sub-genital plate: *N. leroiana* (Klapálek, 1911), *N. camerunensis* (Enderlein, 1909*a*), *N. kunenensis* (Barnard, 1934), *N. didita* (Enderlein, 1909*a*), *N. excisa* (Klapálek, 1923), *N. nigricauda* (Klapálek, 1923), and *N. laticollis* (Klapálek, 1923). *N. africana* (Klapálek, 1910) is described as having the eighth sternum weakly drawn out, but Klapálek (1923) considered *N. camerunensis* a synonym of this species although the original description of *N. camerunensis* stated that no plate was present. Similarly *N. sjöstedti* was originally described as having no plate (Klapálek, 1910), but later was redescribed (Klapálek, 1912) as having a more strongly chitinized patch on the eighth sternum, and later still (Klapálek, 1923) it was suggested that *N. conradti*, of which Enderlein (1909*a*) figured the eighth sternum as bearing a small emarginate lappet, was a synonym of *N. sjöstedti.* Needham (1920) described the subgenital plate of *N. dubia* as a small

Table I.—*The principal features of the male genitalia described in various species of* Neoperla *from Africa. The reference in the last column is to the paper, or papers, in which the male genitalia are described.* N. dubia *has been somewhat differently described by Klapálek and Needham.*

Species.	7th tergum bearing—	8th tergum bearing—	9th tergum bearing—	Author.
africana	triangular three pointed process	triangular patch of denticles	denticles laterally	Klapálek, 1910 and 1923.
arambourgana	no process	tongue-shaped process	?	Navás, 1936.
bottegoana	short rectangular process	?	?	Navás, 1923.
dubia	nose-shaped process covered with pointed teeth	small projection	? no denticles	Klapálek, 1909 and 1923.
dubia	flattened backwardly directed three-pointed process	?	denticles laterally	Needham, 1920.
excisa	trapezoidal process	forwardly bent process	?	Klapálek, 1909 and 1923.
kunenensis	conical backwardly projecting process	rectangular patch of denticles	denticles laterally and centrally	Barnard 1934
lacroixi	large pyramidal backwardly pointing process ending in teeth	?	denticles laterally	Lestage, 1921.
leroiana	only denticles	forwardly directed process with teeth in front	? no denticles	Klapálek, 1911.
needhami	only denticles	conical forwardly directed process	no denticles	Needham, 1920.
nigricauda	wide triangular process with several points	triangular patch of denticles	denticles laterally	Klapálek, 1923.
sjöstedti	simple triangular projection	projection with teeth in front	?	Klapálek, 1910 and 1923
transvaalensis	only denticles	projection with teeth in front	no denticles	Barnard, 1934

emarginate lappet, and stated that the eighth sternum of *N. needhami* is slightly emarginate and more heavily chitinized in the middle. Finally Enderlein (1909*b*) described *N. transvaalensis* as having no sub-genital plate, but Klapálek (1923) stated that the eighth sternum bears a round lappet. Barnard (1934) has shown that the effect seen by Klapálek was due to shrinkage, his specimens not having been relaxed. It would therefore appear that at least some of the differences described between the various species have been due to the examination of unrelaxed dried specimens.

(7) *The eggs.*—These have been described by Barnard (1934) and Needham (1920), and the latter has described a specific difference between the eggs of *N. needhami* and *N. dubia.*

(8) *The male genitalia.*—These have been described in detail by all authors who have described species from male specimens in the present century, with the exception of Navás, who usually made no mention of genitalia, and in a few species did not even mention the sex of the specimen he was describing. Klapálek in particular has given much detail of the genitalia, and has described species as distinct if they differed in very small particulars. Apart from this point, however, the male genitalia appear to offer good specific characters in this genus, as in other genera of Plecoptera. The described species fall into distinct groups according to whether there is a process on the seventh or eighth tergum, or on both. Each group can then be subdivided according to the shape of these processes, and other details, including the length of a pair of forwardly directed horns on the tenth tergum and the shape of a patch of denticles on the eighth and ninth terga. Table I summarises the salient features of the genitalia of these species in which they have been described or figured, and it will be seen that, although some of the species are closely similar, and although one has been differently described by two different authors, most appear to be clearly distinguishable.

From this review, therefore, it would seem that the male genitalia were likely to offer the most satisfactory characters for distinguishing African species of *Neoperla* from one another.

Specimens Available for Study.

The following is a list of the specimens of *Neoperla* which have been available to me for study. The letters in brackets refer to the collections to which the specimens belong. (B.M.) = British Museum; (C.N.) = Coryndon Museum, Nairobi; (C.I.) = Commonwealth Institute of Entomology; (R.R.D.C.) = River Research and Development Centre, Kenya; (J.A.) = Dr. J. Aubert, Musée Zoologique, Lausanne; (I.U.) = Institut pour la Recherche Scientifique, Uvira, Belgian Congo; (J.H.) = Dr. J. Hanson, University of Massachusetts; (C.U.) = Cornell University; (N.H.) = my own collection, most of which has since been presented to the British Museum. Specimens marked with an asterisk are preserved in alcohol, the rest being pinned.

Ivory Coast: ♀* Le Banco, 7.vii, lumière (*Delamere-Debouttville*) (J.A.); ♂* Le Banco, 16.vii.1945, à la lumière (*Delamere-Debouttville*) (J.A.); ♀* Le Banco, 28.vii (*Delamere-Debouttville*) (J.A.); ♂* Le Banco, 31.vii.1945, au fauchage (*Delamere-Debouttville*) (J.A.).

Gold Coast: ♂ near Accra, 1919 (*Mrs. W. Smith*) (B.M.); ♀ Wassau Territory, 1901 (*Dr. S. H. Jones*) (B.M.); ♀ Obuasi, Ashanti, 12.vii.1907, on table near lamp (*Dr. W. M. Graham*) (B.M.).

Sierra Leone: ♂ Gongo, 11.iv.1909 (*A. Pearse*) (B.M.); 16 ♂ 11 ♀ Njala, several months between 1925 and 1935, several collected at light (*E. Hargreaves*) (C.I.); ♂ Sembehun, 1925, at light (*E. Hargreaves*) (C.I.).

Nigeria: ♀ Ibadan, 8.vii.1923 (C.I.); ♀ Oshua River, 17.v.1924 (*F. L. Golding*) (C.I.); 2 ♀ Horin (*F. L. Golding*) (C.I.): ♀ Kogin, Sirikin Pawa, xi.1910 (*J. W. Scott Macfie*) (B.M.); ♀ Zunguru, x.1910 (*J. W. Scott Macfie*) (B.M.); 2 ♀ Oban District, 1910 (*P. A. Talbot*) (B.M.).

Cameroons: 20 ♂ 9 ♀ Kumba, 18–20.x.1949, at light (*W. Crewe*) (N.H.); ♂ Victoria, vii.1916–viii.1917 (*F. H. Fitzroy*) (B.M.); ♀ Yabassi District, lat. 4°N., long. 10°E. xii.1937, dry season (*F. G. Marfield*) (B.M.).

Belgian Congo : ♂* Riv. Tshinganda, Bunyakiri, 26.iii.1950, éclos 27.iii.1950 (*G. Marlier*) (I.U.) ; ♀* Riv. Mushuva, Kalonge, 14.xii.1949 (*G. Marlier*) (I.U.) ; ♂♀* Riv. Tshinganda, Bunyakiri, 27.iii.1950 (*G. Marlier*) (I.U.) ; ♀ Riv. Nyabaronge, Bunyakiri, 28.iii.1950 (*G. Marlier*) (I.U.) ; 2 ♀* Riv. Liviru, Katana, 15.xii.1949 (*G. Marlier*) (I.U.) ; ♀* Mioshi Bitale, 23.iii.1950, dans ruisseau (*G. Marlier*) (I.U.) ; 6 ♂ 12 ♀* Affl. Ruzizi, Bugarama, 21.vii.1949 (*G. Marlier*) (I.U.) ; ♀* Riv. Nyabaronge, Katana, 16.xii.1949 (*G. Marlier*) (I.U.) ; ♂* Ruisseau près de Gîte Meshe, 3.iv.1950 (*G. Marlier*) (I.U.) ; ♀* Le Congo Fl. entre Coq. et Stan. iv.1949 (*M. Laurent*) (I.U.) ; 2 ♀* and one specimen with no abdomen Riv. Luberizi, Lemarol, 17.vii.1950 (*G. Marlier*) (I.U.) ; ♀* Tang de Kanare, 15.vii.1950 (*G. Marlier*) (I.U.).

Uganda : ♀ Banks of Nile near Kakindu, 3400 ft., 24–25.viii.1911 (*S. A. Neave*) (B.M.) ; ♂ ♀ Jinja, vi.1949 (*E. Pinhey*) (C.N.) ; 2 ♂ ♀* Owen Falls, Jinja, R. Nile, 16.vii.1949 (*R. H. Lowe*) (N.H.) ; 8 ♂ 7 ♀* Jinja Bridge, 21.00 hrs., 3.viii.1949 (*R. H. Lowe*) (N.H.) ; ♀ W. Busoga, 14.iv.1926 (*G. D. H. Carpenter*) (C.I.) ; ♀ W. Bugishu, 7000–9000 ft., xii.1928 (*G. D. H. Carpenter*) (C.I.) ; ♂ Bulicheke, x.1931 (*G. H. E. Hopkins*) (C.I.) ; ♂ Bubulu, x.1938 (*T. H. C. Taylor*) (C.I.).

Kenya : 3 ♂ North Kibwezi, 3000 ft., i.1950 (*J. G. Williams*) (C.N.) ; ♀ N.W. Mau, 8000–10,000 ft., 1.ii.1946 (C.N.) ; ♀ Sagana R. Camp, 7400 ft., xii.1942 (*H. Copley*) (C.N.) ; ♂ ♀* R.R.D.C. Sagana River, 23.iii and 22.ix.1949 (*V. D. van Someren*) (R.R.D.C.) ; 2 ♀ Nyeri, vi.1949 (*E. Pinhey*) (C.N.) ; ♂ Thika road, Nairobi, vii.1950 (*E. Pinhey*) (C.N.) ; ♂ Mara River, 5500 ft., i.1950 (*J. G. Williams*) (C.N.) ; ♂ 2 ♀ Ilala, Maramas Dist., 4500 ft., 18–21.vi.1911 (*S. A. Neave*) (B.M.) ; ♀ S. foot and slopes of Mt. Elgon, 5100–5800 ft., 8–13.vi.1911 (*S. A. Neave*) (B.M.) ; ♂ ♀ Gura River (*H. Copley*) (N.H.).

Tanganyika : ♂ Amani, xi.1904, am Licht (C.I.) ; ♀ Amani, vii.1945 (*T. H. E. Jackson*) (C.I.) ; 2 ♀ Sigi, near Amani, 1500 ft., 10.x.1937 (*E. Burtt*) (B.M.) ; ♀ Tanga, 10–14.xii.1916 (*W. A. Lamborn*) (B.M.) ; ♀ Morogoro, 15.i.1917 (*A. Loveridge*) (B.M.) ; ♂ Vy Ruaha R., 18–21.xii.1910 (*S. A. Neave*) (B.M.).

Angola : 3 ♂ 8 ♀ Quirimbo, v.1934 (*K. Jordan*) (B.M.) ; ♀ Luimbale, Mt. Moco, 1800–1900 m., 20.iii.1934 (*K. Jordan*) (B.M.).

Rhodesia : ♂ Lower Luangwa R., 1600–1800 ft., 4–13.x.1910 (*S. A. Neave*) (B.M.) ; ♀ Mazoe R., Shamva, 25.x.1947 (*E. Pinhey*) (C.N.) ; ♀ Chirinda Forest, Gazaland, 3600 ft., 16.x.1905 (*G. A. K. Marshall*) (B.M.) ; ♂ De Beer's Ranch, Shangani, v.1932 (*J. Ogilvie*) (C.I.).

Nyasaland : ♂ Mlangi Boma, 2400 ft., 26–30.iv and 3–5.v.1910 (*S. A. Neave*) (B.M.) ; ♂ between Fort Mangoche and Chikala Boma, about 4000 ft., 20–25.iii.1910 (*S. A. Neave*) (B.M.) ; 2 ♂ (*Dr. J. E. S. Old*) (B.M.) ; 7 ♀ Mlanzi, various dates 1912–1914 (*S. A. Neave*) (B.M.) ; ♀ Ruo Valley, 2000 ft., 14.xii.1913 (*S. A. Neave*) (B.M.).

Natal : ♀ (B.M.) ; 4 ♀ National Park, iii.1932 (*J. Ogilvie* and *Miss A. Mackie*) (C.I.).

Cape Province : ♂ Port St. John, Pondoland, 25–31.iii.1923 (*R. E. Turner*) (B.M.) ; ♀ Umtata, Transkei, 18.ii–18.iii.1923 (*R. E. Turner*) (B.M.).

United States of America (*N. clymene*) : ♂* Josephine Creek, Highlands Co., Fla, iii.1949 (*J. F. Hanson*) (J.H.) ; ♂* N. Waterboro, Me., 18.vi.1939 (*J. F. Hanson*) (J.H.) ; 7 ♂ 2 ♀* No data (C.U.).

Methods.

It will be seen from the above list that there are five series of more than ten specimens collected from the same place. These are from Njala, Sierra Leone ; Kumba, Cameroons ; Quirimbo, Angola ; Jinja Bridge, Uganda ; and Bugarama, Belgian Congo. Incidentally it may be pointed out that Kumba is the same place as Johann Albrechtshöhe, the type locality of *N. laticollis* and *N. nigricauda.* These series have been of great value. Each was examined to determine how much variation there was in the various characters which have been regarded as specific, and the results of this work were then applied to the whole collection. Each specimen in each series was examined for coloration, size, distance apart of ocelli, ratio of width to length of pronotum, wing venation and genitalia, and the eggs in the oviducts or adhering to the abdomens of many of the females were also examined. Most of these characters were also examined in the rest of the specimens available. The abdomens of all pinned males were examined after clearing in hot caustic potash solution, and several of the female abdomens were cleared in the same way.

Most of the figures illustrating this paper were drawn with the aid of a projector, and cleared specimens were used where necessary. Fig. 4G, H, I, J, K and L, were, however, sketched with the aid of a micrometer eye-piece, as the specimens could not be cleared. In the drawings of the genitalia no attempt was made to illustrate the numerous hairs which were present.

Examination of the Specific Characters.

(1) *Coloration.*

The coloration of the Bugarama series was found to be fairly uniform ; the ground-colour was yellowish, and the ocelli were each surrounded by a clear black spot. The tibiae were slightly darkened at the base. Most specimens of the Jinja series were similar to the above, but in three specimens the ocellar spots were fused, and in some the distal halves of the femora were also slightly darkened. The antennae and cerci in both series were pale. The Quirimbo series was slightly darker in general colour, and the ocellar spot was more variable, being divided in some, but fused into a variably shaped single spot in most specimens. The legs of some specimens were yellowish, but in others were variously darkened. The Njala series showed the same general variation, but to a slightly greater extent, the ocellar spot, for instance, forming a bar almost across the width of the head in one specimen, and the legs, cerci and antennae varying from yellow to almost black. The Kumba series was more variable still, and the colour contrast between light and dark was more striking. This is possibly because the specimens were not so old as the other two pinned series, which may have faded. Here the ocellar spot varied from two separate spots to a bar right across the width of the head. The antennae and cerci varied from yellow, through dark at the tip, to all black. The legs varied from yellow with a slight darkening at the base of the tibia, through specimens in which the femoro-tibial joint was darkened, to specimens in which the tibiae and distal halves of the femora were black. The specimens of this series would therefore, fall into several species if identified with the key given by Klapálek (1909). This series covers almost all the colour variations of the described species, and, apart from the fact that a few specimens in the collection had very dark wings and bodies, it also covers the range of coloration throughout the collections. It is noticeable that at least one of the very dark specimens, from the Belgian Congo, was collected at the same time as a very pale specimen.

(2) *Size.*

The ranges of the lengths of the fore wings in the five series were found to be as follows. The lengths are given in mm.:

	Males.	Females.
Jinja	13½–14½	15–18½
Quirimbo	11½–12	12½–15½
Njala	7 – 9½	9½–15
Bugarama	13 –14	16 –18
Kumba	9½–11	11½–14½

Size would appear therefore to be as continuously variable as coloration, but in each locality the males are generally smaller than the females. The range of the lengths of the fore wings of the whole collection was : males 7–14½ mm., females 9–22 mm. The smallest female is from Oban, Nigeria, and the largest from Kalonge, Belgian Congo. The range of size in any one series, or of specimens from any one territory, appeared to be continuous, and it will be noted that the size range of the collection at my disposal was slightly greater than the size range of the described species. There seems to be a certain amount of correlation between geographical distribution and size. The largest specimens of both sexes were from territories in Central Africa, and the smallest from territories on the West Coast. Specimens from southern territories were mostly intermediate in size, and intermediate-sized specimens were present in the collections from most territories. Males with fore wings less than 10 mm. long were present only in collections from the Ivory Coast, Gold Coast, Sierra Leone and the Cameroons, while males with wings more than 12 mm. long were present only in collections from the Belgian Congo, Uganda, Kenya, Tanganyika and Rhodesia. Similarly females with fore wings less than 12 mm. long were present only in collections from the Ivory Coast, Gold Coast, Sierra Leone, Nigeria, Cameroons and the Belgian Congo, and females with wings more than 17 mm. long were present only in collections from the Belgian Congo, Uganda, Kenya and Cape Province. There were, however, too few specimens available to do more than indicate the possibility of such a geographical size-distribution.

(3) *Distance Apart of the Ocelli and their Distance from the Eyes.*

The distance of the ocelli from the eyes is best expressed as the ratio distance of the ocelli from the eyes divided by the distance apart of the ocelli. In the five series this ratio was found to vary as follows :

Jinja	1·5–2·6	Bugarama	1·7–3·0
Quirimbo	1·4–2·6	Kumba	1·1–2·2
Njala	1·1–2·8		

The variation in each series was continuous. In view of this variation and of the similar variation shown above to occur in *N. clymene* it seems that this character cannot be used to separate species of *Neoperla*. The range of this ratio in all the specimens available was found to be 0·8–3·2, which, apart from the fact that no specimens were found in which the ocelli are almost touching,

TABLE II.—*Details of the wing venation of specimens in the Jinja and Kumba series showing numbers of cross-veins and branches of the first cubital (Cu_1) and radial sector (Rs) and whether the posterior branch of Rs arises from (+) or beyond (—) the anastomosis.*

Series.	Sex.	Right fore wing.							Left fore wing.							Right hind wing.					Left hind wing.				
		Sc cross-veins	C cross-veins.	M–Cu_1 cross-veins.	Cu_1–Cu_2 cross-veins.	branches of Cu_1.	branches of Rs.	Rs branching in anast.	Sc cross-veins.	C cross-veins.	M–Cu_1 cross-veins.	Cu_1–Cu_2 cross-veins.	branches of Cu_1	branches of Rs.	Rs branching in anast.	Sc cross-veins.	C cross-veins.	Cu_1–Cu_2 cross-veins.	branches of Rs.	Rs branching in anast.	Sc cross-veins.	C cross-veins.	Cu_1–Cu_2 cross-veins.	branches of Rs.	Rs branching in anast.
Jinja	♂	8	5	7	6	3	4	+	8	4	8	5	3	4	+	4	2	4	4	—	3	3	5	4	—
	♂	7	3	6	4	2	4	—	7	3	6	4	3	4	—	5	2	4	3	—	4	3	4	3	—
	♂	8	3	7	4	2	4	+	6	3	5	5	3	4	+	5	3	4	3	—	5	4	4	3	—
	♂	8	5	8	7	3	4	+	8	4	8	5	3	4	+	6	4	5	4	—	4	3	6	4	+
	♂	8	4	7	4	3	4	+	7	3	7	5	2	4	+	4	?	4	4	—	5	?	3	5	+
	♂	7	5	7	3	3	4	—	8	3	8	4	3	4	+	4	3	4	3	—	5	4	4	3	—
	♂	7	3	6	4	2	4	+	8	2	6	4	2	4	+	6	?	5	3	—	5	?	5	3	—
	♂	10	4	7	5	2	4	+	8	4	6	5	3	4	+	7	?	4	?	+	7	?	5	4	+
	♀	10	5	8	5	2	4	+	7	4	8	5	3	4	+	4	?	5	4	+	4	?	5	3	—
	♀	8	5	7	6	3	4	—	10	5	7	6	3	4	—	6	4	4	4	—	7	5	6	3	—
	♀	10	6	7	6	3	4	+	11	4	6	5	2	4	+	6	3	5	4	—	5	3	4	4	+
	♀	8	4	7	4	2	5	+	8	4	8	4	3	4	+	5	2	4	4	+	6	4	5	4	—
	♀	11	4	8	5	3	4	+	9	3	8	5	3	5	+	4	?	4	4	—	5	?	4	4	+
	♀	8	4	7	4	3	4	+	8	?	6	5	3	4	+	5	?	4	4	+	4	?	5	4	+
	♀	8	4	7	5	3	4	—	10	4	7	5	4	4	—	6	?	4	3	—	6	?	5	4	—
Kumba	♂	11	2	8	5	2	3	—	12	3	7	5	2	3	—	5	3	5	3	—					
	♂	12	3	6	5	2	4	—	12	3	7	5	2	4	—	5	3	6	3	—					
	♂	11	3	5	4	2	3	+	12	3	6	3	2	3	—	2	3	5	3	—					
	♂	10	3	8	5	2	3	—	13	2	7	5	2	3	—	6	4	3	3	—					
	♂	10	3	6	4	2	3	—	12	2	6	4	2	3	—	5	2	4	3	—					
	♂	7	3	7	5	2	3	+	11	3	7	4	2	3	+	3	2	7	3	—					
	♂	10	2	7	6	2	3	+	12	3	8	5	2	3	—	2	1	5	3	—					
	♂	12	4	9	5	1	4	—	12	3	7	5	2	3	—	3	0	4	3	—					
	♂	11	3	6	5	2	4	—	11	3	6	5	2	4	+	3	2	4	4	+					
	♂	7	2	7	4	2	4	+	9	3	6	4	2	4	+	3	1	3	4	—					
	♂	14	2	7	7	2	3	+	13	2	7	4	2	3	+	4	3	6	3	—					
	♀	11	2	7	6	2	3	+	12	3	7	6	2	3	+	5	3	5	4	+					
	♀	8	1	6	4	2	4	—	8	3	6	4	2	3	—	2	3	4	3	—					
	♀	10	3	7	5	2	3	+	10	3	7	5	2	3	+	6	3	4	3	—					
	♀	12	4	10	5	2	3	—	10	3	8	5	2	3	+	5	3	6	3	—					
	♀	12	3	9	5	2	4	—	11	3	8	6	2	3	—	4	1	4	3	—					
	♀	12	3	9	5	2	4	—	11	3	8	6	2	3	—	4	1	4	3	—					
	♀	15	3	8	6	2	4	+	14	3	8	7	2	4	+	5	3	5	3	—					
	♀	12	3	7	4	2	3	—	12	2	7	5	2	4	—	4	3	3	3	—					
	♀	13	2	8	6	2	3	—	14	3	9	6	2	4	+	7	4	5	3	—					

as described in *N. transvaalensis* by Tillyard (1931), covers the range of all the described African species. The relative sizes of the ocelli were also found to be very variable, and the same order of variation was found when the distance between the ocelli was expressed, as some authors have expressed it, in terms of the diameter of the ocellus.

(4) *Ratio of Width to Length of Pronotum.*

The range of the ratios of width to length of pronotum in the Kumba series was found to be 1·31–1·67, in the Njala series 1·29–2·07. The latter series therefore covers the whole range of variation in the described species. As stated above, some of this variation was probably due to shrinkage and distortion, but it is clear that this ratio is in fact really variable, as the range was found to be 1·68–1·97 in the Jinja series, and 1·67–1·95 in the Bugarama series, both of which are preserved in alcohol and so, presumably, are not distorted.

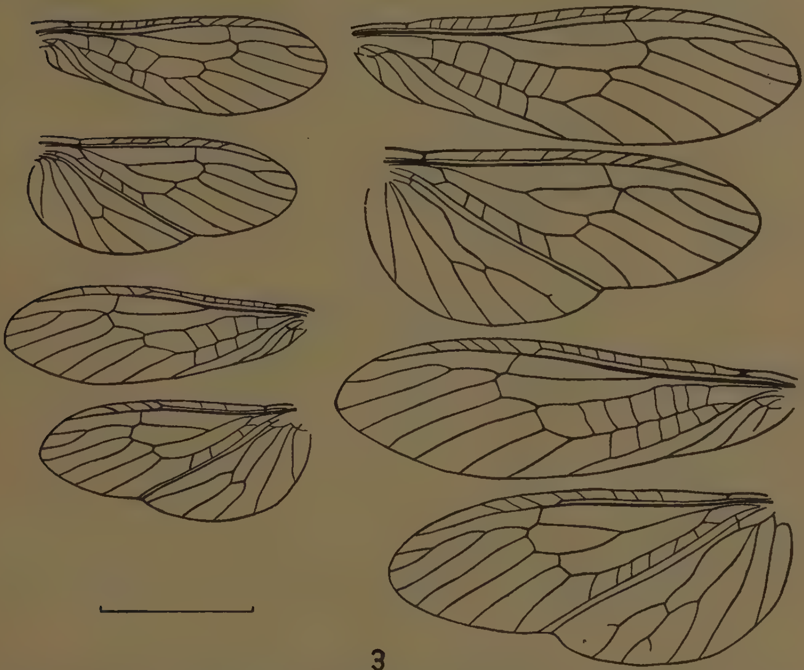

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Fig. 3.—Wings of a male (left) and a female (right) *Neoperla* from Njala, Sierra Leone. The line represents 5 mm.

(5) *Wing Venation.*

Table II gives details of the wing venation of the Jinja series and of several specimens of the Kumba series. It will be seen that the numbers of cross veins and of the branches of the first cubital vein and radial sector were very variable, and that they may vary on the two sides of the same insect. The same applies to the point of origin of the posterior branch of the radial sector, which may arise from or beyond the anastomosis. The same sort of variation was found in the Njala series, the wings of two specimens of which are shown in fig. 3. From this it appears obvious that no attempt to separate species of

Neoperla on the basis of wing venation can be justified, and that the use of it in the separation of species by Klapálek and Navás is invalid.

(6) *The Sub-genital Plate* (*eighth sternum*) *of the Female.*

The great majority of the specimens available for study were found to have a straight posterior margin to the eighth sternum, but in a few it was found to be slightly drawn out in the middle. In the Quirimbo series, however, some specimens were found in which the margin was slightly emarginate and more heavily chitinised just inside the vagina. Fig. 4B–F show the range of variation in outline found in this series. These few specimens would on this character be referable to several of the described species. In addition one specimen from Kenya (fig. 4A) was found which had a deep emargination, and four specimens from the Belgian Congo (fig. 4G–J) had small lappets, three of which were more or less emarginate in the middle. The fact that, in the pinned specimens, these structures were not merely due to shrinkage was confirmed by relaxing them in caustic potash solution. These various types occurred at random in the collection, and they seem to form a more or less continuous series of variation. The variation in chitinisation is also considerable, and some specimens with an entire sternum were heavily chitinised just inside the vagina. As specimens with variously developed sub-genital plates were not found to differ consistently in any other particulars, it would appear that these small differences in the eighth sternum are merely individual, as is indeed foreshadowed by some of the conclusions of Klapálek (p. 90).

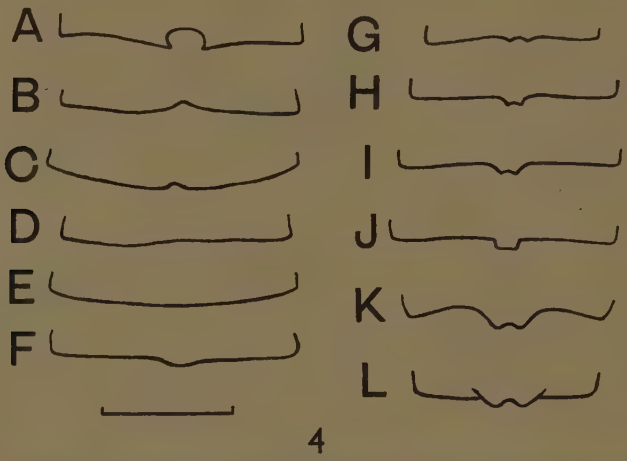

Fig. 4.—Outlines of the posterior margins of the eighth sterna (sub-genital plates) of females of *Neoperla*. From: A. Mount Elgon, Kenya. B–F. Njala, Sierra Leone. G. R. Congo, Belgian Congo. H. Katana, Belgian Congo. I and J. Limarol, Belgian Congo. K and L. U.S.A. (*N. clymene*). The line represents 1 mm.

While examining these specimens it was noted that the spermatheca in all in which it could be seen was a long narrow tube, usually coiled up in the eighth segment. No sign of a spermatheca could be found in specimens which were full of ripe eggs. Perhaps it was this organ which Newman (1839) described as a curled up nematode in the type-specimen of *N. spio*. A few female specimens were, however, examined for nematodes and a few very small encysted specimens were found in the fat body, several being present in each specimen.

(7) *The Eggs.*

Several specimens were found with eggs attached to the abdomen, and most of these resembled the eggs of *N. transvaalensis* as figured by Barnard (1934) and of *N. needhami* as figured by Needham (1920). In the Quirimbo series, however, one female was carrying eggs of this sort, and another was carrying eggs with spiral striae similar to those described in *N. dubia* (Needham, 1920). The eggs in the oviducts of this series were therefore examined closely, and were found to vary considerably even within one specimen, as is shown in fig. 5. The same was found to apply to the Kumba series, where the female sub-genital plate was more uniform. It is doubtful how much significance can be attached to these differences, as it is unknown how much the shape and wrinkling of the chorion is affected by preservation. In the absence therefore of other characters separating the females the eggs can scarcely be used for the separation of species.

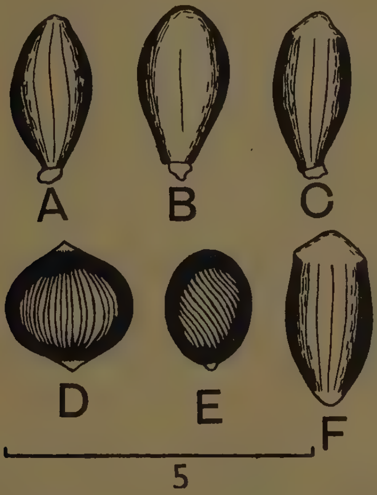

Fig. 5.—Eggs from the oviducts of females of *Neoperla* from Njala, Sierra Leone. A–C. Eggs from one specimen. D–F. Eggs from three other specimens. The line represents 1 mm.

(8) *The Male Genitalia.*

Examination of the male genitalia of all the specimens, after maceration in caustic potash in the case of the dried specimens, showed that all the described types of genitalia were represented. They occurred in a haphazard manner throughout the collection, several types being sometimes present in the same series. Fig. 6 shows the dorsal and profile views of the genitalia of three

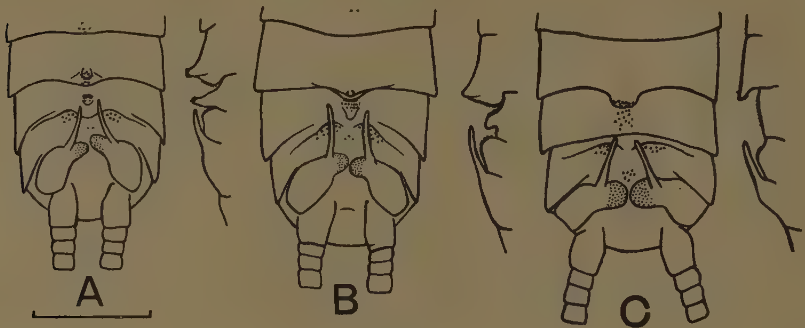

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FIG. 6.—Dorsal and profile views of the male genitalia of three specimens of *Neoperla* collected in i.1950 at North Kibwezi, Kenya. The line represents 1 mm.

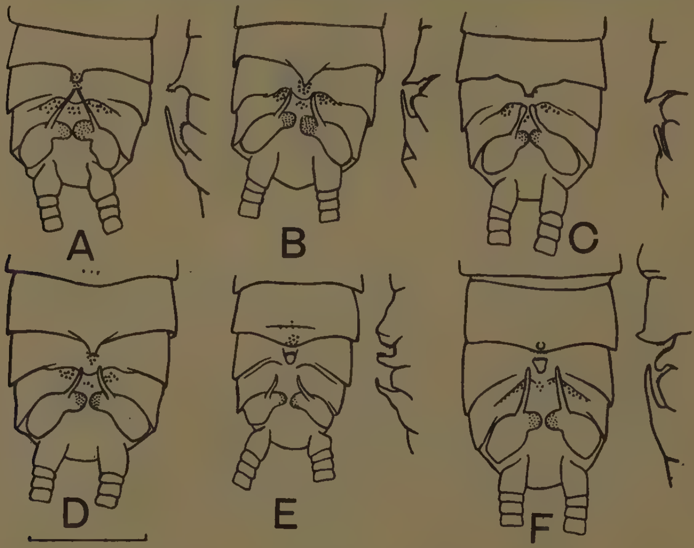

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FIG. 7.—Dorsal and profile views of the male genitalia of specimens of *Neoperla*. From: A–E. Kumba, Cameroons. F. Port St. John, Pondoland, Cape Province. The profile of D was similar to that of B. The line represents 1 mm.

specimens collected on the same day at North Kibwezi, Kenya. Specimen A is very similar to *N. sjöstedti*, specimen B to *N. dubia*, and specimen C to *N. kunenensis*. Otherwise these three specimens resembled one another closely in size, colour and general appearance. Similarly fig. 7A–E shows several of the genitalia of the Kumba series. Here, again, the various specimens closely resembled various described species. Finally fig. 8 shows the genitalia of several of the Njala series. It can be seen that these form a continuous series of variation from the *kunenensis* type to the *excisa-leroiana* type, and that the other described species are all intermediate between these. Examining the figures in succession from A to I it will be seen that—

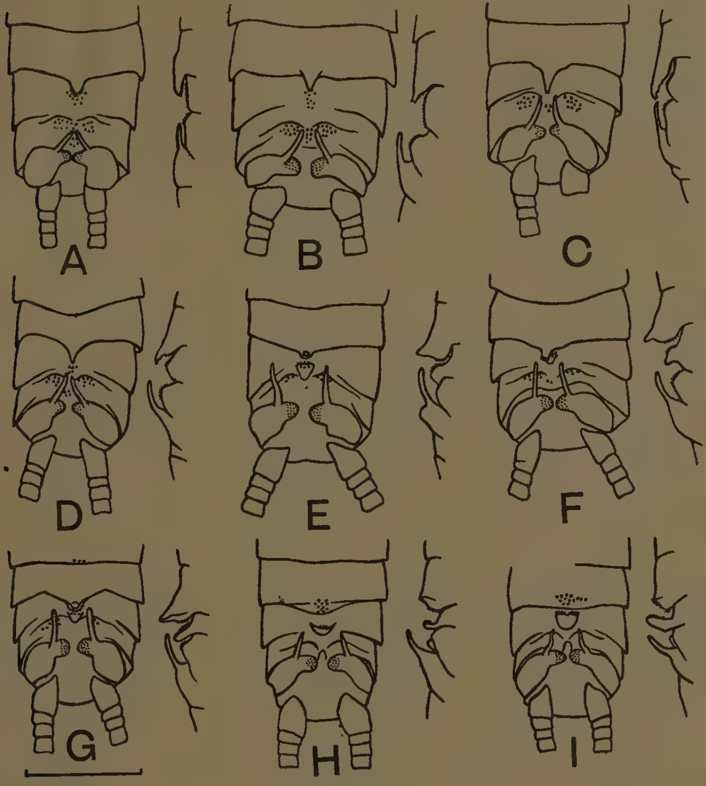

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FIG. 8.—Dorsal and profile views of the male genitalia of nine specimens of *Neoperla* from Njala, Sierra Leone. The line represents 1 mm.

1. The process on the seventh tergum starts as a flat lappet and becomes a backwardly directed conical process with a variable number of points; this process then becomes more or less vertical and decreases in height, becoming a wide ridge and finally disappearing. Meanwhile the teeth on the ventral (posterior) side of the process slide, as it were, down the process until they come to lie as denticles on the centre of the posterior edge of the tergum.

2. As the change outlined above occurs, the eighth tergum, which at first bears a variously shaped patch of denticles, becomes slowly more arched in the centre, until it comes to bear a distinct process, with anteriorly pointed teeth, which ultimately becomes higher than the steadily reduced process on the seventh tergum.

3. The ninth tergum bears denticles on the lateral humps and centrally when there is a large process on the seventh tergum, but that as this process decreases, and that on the eighth tergum increases, in height, these denticles tend to disappear, first centrally and then from the lateral humps. That they may, however, persist is shown in fig. 6A and 7F, and by Barnard's figure of *N. kunenensis*.

4. The length and shape of the forwardly directed horns of the tenth tergum are very variable, as is the shape of the inner lobes of the two sclerites of this tergum.

5. When the process on the eighth tergum is large, a small process appears posteriorly between the humps on the ninth tergum.

A further point of variation is the presence in some specimens (fig. 6A and 7B) of a few denticles on the posterior edge of the sixth tergum.

It would appear that what is required, functionally, of this complex of processes, teeth and denticles, is that a process on the seventh or eighth tergum can be brought to bear on to a patch of denticles or on to a similar process. Unfortunately nothing is known about how this apparatus functions.

The Njala series alone covers almost all the types of genitalia found or described, but it will be seen from fig. 6C that some specimens were found in which the lappet on the seventh tergum was wider than any found in the Njala series. This wide lappet was present in many specimens of the Jinja and Bugarama series. Both of these series were fairly uniform, the chief variations being in the width of the lappet, the shape of the patch of denticles on the eighth tergum, and the length and shape of the processes on the tenth tergum.

A further point requiring mention is the shape of the inner lobes of the sclerites of the tenth tergum. These have already been shown to be very variable, but Klapálek (1923) figured *N. excisa* as having no such lobes. This effect was seen on several specimens before they were relaxed, and was due to the folding inward of the lobes by shrinkage. It seems certain that Klapálek examined an unrelaxed specimen.

Dr. Hanson (*in litt.*) suggested to me that the aedeagus might provide useful specific characters in this genus, but careful examination of all the specimens which were cleared showed no good differences in structure. The only variation observed was one of width, the aedeagus tending to be wider in specimens with a wide lappet on the seventh tergum.

This is, I believe, the first time that it has been suggested that the male genitalia of any genus of stoneflies are unsuitable for specific determination because of great and continuous variation. Generally speaking these structures are extremely constant and form the most important means of distinguishing species in other genera. Because of this the geographical occurrence of the various types of genitalia found was carefully studied to see whether or not this supported the implication that only one very variable species was being studied.

The male genitalia of African Neoperlinae figured in this paper, and described and figured by previous authors, can be placed in seven somewhat overlapping groups, to one of which it is possible to assign most specimens. These are:

A. Specimens with a wide lappet, bearing denticles ventrally, on the seventh tergum, and with only denticles on the eighth tergum (fig. 6C).

B. Specimens with a narrow lappet, bearing denticles ventrally and sometimes with spines round the edge, on the seventh tergum, and with only denticles on the eighth tergum (fig. 8A).

C. Specimens with a backwardly directed conical process, ending in two to a few points and bearing denticles at the base, on the seventh tergum, and with only denticles, or a very small hump bearing denticles, on the eighth tergum (figs. 8B and C).

D. Specimens with a more or less backwardly directed simple process, ending in a simple point and bearing denticles at the base, on the seventh tergum, and with only denticles, or a very small hump bearing denticles, on the eighth tergum (fig. 8D).

E. Specimens with an upwardly directed conical process, usually ending in a simple point but occasionally with a few points, and bearing denticles at the base on the seventh tergum, and with a medium-sized hump or process, bearing denticles anteriorly, on the eighth tergum (figs. 8E and F).

F. Specimens with a more or less small upwardly directed process, usually ending in a simple point but occasionally with a few points, and bearing denticles at the base, on the seventh tergum, and with a fairly large process, bearing denticles or points anteriorly, on the eighth tergum (fig. 8G).

G. Specimens with no process, but only denticles, and sometimes with a transverse ridge, on the seventh tergum, and with a large process, bearing points anteriorly, on the eighth tergum (figs. 8H and I).

These are in fact merely stages in the steady progression outlined above.

Specimens of each of these genitalia types were found, or have been described from the following territories. The number of specimens from each territory in each group is shown in brackets:

A. Belgian Congo (4), Uganda (11), Kenya (1).

B. Sierra Leone (3), Cameroons (1), Belgian Congo (3), Uganda (1), Kenya (2), Nyasaland (2), South-West Africa (*N. kunenensis*).

C. Ivory Coast (1), Sierra Leone (5), Cameroons (12 and *N. dubia* and *N. nigricauda*), French Congo (*N. lacroixi*), Belgian Congo (2) and *N. dubia*).

D. Ivory Coast (1), Sierra Leone (1), Cameroons (5 and *N. africana*), Fernando Po (*N. africana*), Kenya (1), Tanganyika (1 and *N. africana*), Angola (3).

E. Sierra Leone (5), Cameroons (2), Kenya (1), Rhodesia (2), Nyasaland (2).

F. Sierra Leone (3), Kenya (1), Tanganyika (1 and *N. sjöstedti*), Cape Province (1).

G. Egyptian Sudan (*N. leroiana*), Ethiopia ? (*N. bottegoana*), Gold Coast (1), Sierra Leone (3), Cameroons (1 and *N. excisa*), Belgian Congo (*N. needhami*), Uganda (1), Kenya (2 and *N. arambourgana*), Transvaal (*N. transvaalensis*).

Making allowance for the fact that very few specimens were available from some territories, it will be seen from the above that each of these genitalia types is very widespread, and that there is no indication of any limited geographical distribution of any of the types.

A point of interest is that the one male specimen available to me from South Africa (fig. 7F) is intermediate between the two species described from South Africa by Barnard (1934). His work was based on only two specimens, and doubtless had he more he would have observed the inconstancy of the male genitalia.

CONCLUSION.

From this study of the chief characters which have been used to separate species of *Neoperla* in Africa, the inevitable conclusion seems to be that only one species has so far been collected there. The only alternative is to postulate a large number of more or less co-extensive species which overlap one another in all characters which have so far been studied. As there is no indication of this, it is proposed that all these forms be referred to one species, which, according to the usual procedure, must bear the name *Neoperla spio* (Newman).

DISTRIBUTION OF *Neoperla spio*.

Neoperlinae, and therefore specimens of *Neoperla spio*, have been recorded from the following territories: Egypt ?, Egyptian Sudan, Ethiopia, Ivory Coast, Gold Coast, Liberia ?, Sierra Leone, Nigeria, Cameroons, Fernando Po, French Congo, Belgian Congo, Uganda, Kenya, Tanganyika, Angola, Rhodesia, Nyasaland, South-West Africa, Transvaal, Natal and Cape Province. The species has been found at high and low altitudes, although Dr. van Someren informs me that in the Sagana River, on Mount Kenya, the nymphs are commonest at 5600 ft., are scanty at 5800 ft. and do not occur at all above 5900 ft. Miss R. H. Lowe failed to find any signs of the species above 10,000 ft. on Ruwenzori. One specimen from Uganda in the Commonwealth Institute collection is, however, labelled as having been taken between 7000 and 9000 ft., and one specimen in the Coryndon Museum is recorded from 7400 ft. on the Sagana River. It seems probable that the upper altitudinal limit of the species may vary from place to place, and that individual specimens may move far from their place of eclosion.

The species apparently occurs in all countries south of the Sahara where there are permanent streams. The one record from South-West Africa is surprising, as this territory is almost all desert and semi-desert, with temporary water-courses, but the specimen was collected on the Kunene River (Barnard, 1934), which forms the northern boundary, and it would seem doubtful if it occurs in other parts of the territory.

Adults have been collected in almost all months of the year, but in view of the variability of climate in Africa, over relatively small distances, this fact gives no indication of whether or not emergence is confined to wet or dry seasons. It seems certain, however, that they are usually active at night, when the humidity is higher than by day. *N. clymene* is also a nocturnal species (Frison, 1935).

A point of interest is that no Plecoptera have been recorded from Madagascar, which is the one place in the Ethiopian Region where a population could become completely isolated, and so perhaps develop into a distinct species. As Norman (1947) has pointed out, however, the distribution of freshwater fishes indicates that Madagascar has been separated from Africa since, at least, the end of the Tertiary Era, and possibly *Neoperla* did not invade Africa until later on. Over the rest of the area the distribution, although extensive, is continuous, and, for an insect which flies actively at night, there are probably no barriers that cannot be circumvented.

Discussion.

The great variability of *N. spio* raises questions of some interest.

Firstly, is this variability, particularly in the male genitalia, characteristic of *N. spio* alone, or does it also occur in other species of the genus ? This raises the whole question of the large number of species of *Neoperla* which have been described from southern and eastern Asia. Many of these, like the species described from Africa, have been described from few specimens, and, where the genitalia have been mentioned, the differences between the species are rather similar to those which were used to separate species from Africa.

Secondly, can *N. spio* be separated morphologically from *N. clymene* of North America? The latter species, which is widely distributed east of the Rocky Mountains, appears to be the only American species of the genus, other specific names having been put into synonymy (Frison, 1935). The male genitalia, as figured by Frison and as shown in fig. 9, are very similar to some forms of these organs found in *N. spio*. There is no indication in the literature of any variation in these organs, and in the nine males available to me the only variation observable was in the detail of the shape of the conical process on the seventh tergum, and the length of the horns on the tenth tergum. In these specimens, however, and in the two females, coloration and wing venation appeared to be as variable as they are in *N. spio*. The colour varied from very dark, with almost black head, antennae, cerci, tibiae and distal halves of femora, to pale yellowish, with only a dark spot round the ocelli and another on the clypeus, and a slight darkening of the posterior edges of the femora and tibiae. Similarly the wing venation was very variable, as is shown in Table III. The wings of opposite sides were not quite the same in any of the specimens, and in some wings the posterior branch of the radial sector arose from, and in others beyond, the anastomosis. There were also many small irregularities in the venation, such as extra or anastomosing cross-veins, as were also found in *N. spio*. The two females both had sub-genital plates (figs. 4K and L), but as Frison's (1935) figure of the tip of the abdomen of this species shows no such plate, this may be a variable character in *N. clymene* also. If,

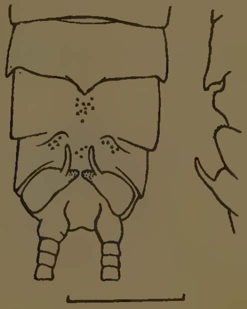

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Fig. 9.—Dorsal and profile views of the genitalia of a male *Neoperla clymene* from N. Waterboro, Me., U.S.A. The line represents 1 mm.

TABLE III.—*The maximum and minimum numbers of various cross-veins and branches of principal veins in the wings of the specimens of* Neoperla clymene *from U.S.A.*

	Fore wing.		Hind wing.	
	Max. no.	Min. no.	Max. no.	Min. no.
Sc cross-veins	12	3	6	0
C cross-veins	4	0	3	1
M–Cu$_1$ cross-veins	7	5	.	.
Cu$_1$–Cu$_2$ cross-veins	7	3	6	3
Branches of Cu$_1$	3	1	.	.
Branches of Rs	3	2	3	2

however, it is not variable, it might serve to distinguish *N. clymene* from *N. spio*, as might the shape of the spermatheca. I have not been able to examine the spermatheca of *N. clymene*.[1] But apart from these doubtful points I have found no character which will clearly separate these two species. I do not wish to imply that they are therefore not separable, as I have too little material of *N. clymene* on which to base any conclusions. It is, however, interesting that, because of the great variability of *N. spio*, these two species, from totally different parts of the world, should resemble one another so closely that an American specimen could not at present be picked out from an African collection.

Lastly, why is *N. spio* so variable, particularly in respect of characters like the genitalia, which have proved to be so reliable in other stoneflies? The continent of Africa is very variable in climate and general ecological conditions, but not more so than North America, where *N. clymene* appears to be less variable at any rate as regards male genitalia. Two explanations appear possible.

In the first place it is known that in Africa, during the Mid-Pleistocene epoch, there was a very arid period preceded and followed by pluvial periods (Worthington, 1940). During this arid period populations of *Neoperla* would presumably have been confined to high areas where streams remained permanent. In these isolated areas, owing to the Sewall Wright effect, each population may have become different from the others, but perhaps not so different as to be unable to interbreed with them. Then later, when mixing again became possible, characters developed by these populations would presumably have combined and recombined, giving many intergrading types. As long as such characters were not greatly deleterious, there seems no reason why they should not have persisted. Such characters may well be details of coloration, which presumably are not of great importance in cryptic nocturnal insects, wing venation, and such things as ocellar distance, details of the proportions of the pronotum and pattern of the egg-chorion. The same may well apply to the genitalia. As suggested above, all that seems to be required, in the male, is a clasping mechanism in the region of the seventh or eighth tergum. In the female the presence or absence of a small sub-genital plate is presumably of little consequence in copulation, as in other stoneflies closely related species vary much in this character. Therefore as long as the genitalia function they presumably have little influence on survival.

---

[1] Since this paper was written I have, through the kindness of Dr. W. E. Ricker of The Fisheries Research Board of Canada, been able to examine the spermatheca of a female *Neoperla clymene* from Georgia, U.S.A. This was found to be a coiled tube closely resembling that found in specimens of *N. spio*. Also the sub-genital plate in this specimen was less developed than in the specimens illustrated in figs. 4K and L, and closely resembled that of the *N. spio* illustrated in fig. 4H. It is clear therefore that the female genitalia do not offer any clear means of distinction between *N. clymene* and *N. spio*.

In the second place *N. spio* appears to be the only Perlid of the Ethiopian Region, and for most of its range the only stonefly. Unlike other stoneflies, therefore, it fills an ecological niche for which there is probably little or no competition. It may therefore be that *N. spio* encounters less selective pressure than other species, as it has no direct competitors. Instances are known where, on islands, several species have apparently arisen from one original species, and it has been suggested that lack of selective pressure has resulted in variation leading to speciation. May it not be that the same thing applies to *N. spio*, which, so far, has only become, or been allowed to remain, very variable, but which may later, or if conditions change, give rise to many species? If, as applies to *N. clymene* in North America, most available stonefly niches were filled by other species of stoneflies, the selective pressure might be too great to allow any one species to be very variable. This point cannot, however, be discussed further because of our lack of knowledge of how competition between allied, or ecologically similar, species occurs.

SUMMARY.

(1) It is shown that all Neoperlinae from the Ethiopian Region belong to the genus *Neoperla* Needham, and that the name *Ochthopetina* Enderlein should be dropped.

(2) It is shown that all the described species of *Neoperla* from Africa, and all the African specimens available for study, belong to one extremely variable species, which must be called *Neoperla spio* (Newman).

(3) *N. spio* is recorded from almost all territories south of the Sahara where there are permanent water-courses. It appears to be the only species of stonefly present in tropical and southern sub-tropical Africa.

(4) It is tentatively suggested that a revision of the species of *Neoperla* from Southern and eastern Asia may show that similar intra-specific variability may also occur there.

(5) Because of the great variability of *N. spio* no satisfactory character has been found which will enable it to be separated from *N. clymene* of North America, but insufficient material of the latter species was available.

(6) The great variability, particularly of the male genitalia, of *N. spio* is discussed, and it is suggested that this may be due to isolation of several populations during an arid period during the Pleistocene, followed by variation and subsequent interbreeding of the populations. It is also suggested that lack of competition with other stoneflies may have allowed the unusual variability of this species to persist.

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ON THE GENERIC CLASSIFICATION OF DERBIDAE (FULGOROIDEA), WITH DESCRIPTIONS OF NEW NEOTROPICAL SPECIES.

By R. G. Fennah.

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With 38 Text-figures.

Introduction and Acknowledgments.

This report deals with a collection of Derbidae made by the writer in the Lesser Antilles, and with a few species which have come to hand from Venezuela, Trinidad and British Guiana. Opportunity is taken to revise certain generic concepts, and to incorporate them, together with new genera, in revised keys.

The writer's thanks are tendered to the authorities of the British Museum for the opportunity of examining Derbidae in the National Collection, and in particular to Dr. W. E. China for his ready assistance on many points of detail, and for the preparation of drawings from type material. Thanks are due also to H. E. Box, Entomologist, Division of Sugar-cane Research, Ministerio de Agricultura y Cria, Venezuela, and Dr. J. Rácenis of the Universidad Central de Venezuela for gifts of derbid material from Venezuela.

Historical Résumé.

In 1841 Westwood erected the genus *Cenchrea* for the reception of a new species, *dorsalis*, and *Patara* for what he considered two new species, *albida* and *guttata*, based on material collected in St. Vincent by Guilding. Fifty-four years later Uhler (1895 : 69) listed all three when reporting on the hemipterous collections of H. H. Smith from the same island, and noted two further species. One of these he described as a new *Cenchrea* (*C. exquisita*), while the other he referred to *Persis fabriciana* Metc. (= *lineata* (F.)). In the present paper four new genera and 27 new species are added to the Lesser Antillean fauna, while 17 new species are described from the mainland and Trinidad. Types of all species discussed have been placed in the British Museum (Natural History).

Higher Taxonomy of Derbidae.

In 1918 Muir divided the Derbidae into two sub-families, Zoraidinae and Derbinae, a disposition which he reaffirmed in 1923 and 1930. These sub-families were separated essentially by a single character, namely the normality or reduction of the cubital area in the wings. In any natural classification such a division, which sets the tribes Zoraidini and Sikaianini fundamentally apart from the remainder (Cenchreini, Rhotanini, Derbini and Otiocerini), necessarily implies that the points of resemblance between genera of each sub-family are due to parallel evolution after an early cleavage into two main stocks. Even if the gap between the "normal winged" and the "reduced winged " condition were utterly bridgeless, there would still be insufficient reason for regarding this difference as so phylogenetically ancient as to antedate the appearance of the many points of resemblance between tribes. The simpler interpretation of the facts would be to regard the aggregate of characters in agreement as evidence of monophyletic affinity, and the single-character difference (resulting from degeneration of a structure in one group) as a later specialisation. As it is, however, the gap between the wing-condition of the two groups can be bridged: indeed, the available evidence favours the conclusion that both wing-shapes occur in the same tribe.

Apart from the shape of the wing, Muir erected one other criterion for his subfamily Zoraidinae, namely, "Tegmina long and narrow." The tegmina of Zoraidini and Sikaianini vary in shape and proportions, even within the limits of a single genus (*Zoraida*). They have certain characters, chiefly venational, by which they can readily be recognised, but these have no common feature which is lacking in other tribes. Excessive elongation and narrowness of the tegmina are not found in all genera of these two tribes: in a few (*Pamendanga* Dist.) the proportions are very similar to those of some Otiocerini and Derbini. When dealing with the genus *Zeugma*, in which the tegmina are typically zoraidine but the wings are similar to those in unspecialised "Derbinae," Muir was compelled to reject one of his subfamily characters. He placed the genus in the latter subfamily (tribe Derbini) and ignored the tegmina. By so doing he effectively narrowed his subfamily distinction to wing characters only.

The transition, by reduction of the cubital and anal areas, from the ampliate wing of a relatively primitive cenchreine derbid, such as *Herpis* or *Cedusa* (or even the anomalous *Vinata*), to the small scale-like stridulatory appendage of the sikaianine *Muiria* is of considerable interest. The first step is the reduction in size (without deformation) of the wing in relation to the tegmina. This stage is represented by the condition in *Zeugma* and *Dysimia*. The second step is reduction of the postcubital area: this is exemplified in *Symidia* and *Pamendanga*. Then follows the excavation of the cubital and anal portion of the wing margin. This may involve no reduction in veins (*Proutista lumholzi* Kirk.), or simplification of Cu_1 and reduction of veins posterior to it (some *Helcita* and some *Diostrombus*). In all these modifications the corrugated and thickened area on the innermost hind margin of the wing does not undergo any reduction, and indeed may slightly enlarge. This modified area, in different degrees of prominence, is present and functional (as part of a stridulatory apparatus) in most genera of Derbidae, and has apparently developed only once in the family. At a more advanced stage the wings may be greatly reduced and the venation represented only by a simple R and M (some *Diostrombus* and most Sikaianini). The limit of reduction is reached where the wing is represented only by a minute lobe bearing the corrugated stridulatory area (*Muiria*).

Each step in this series is quite short (as also are the steps by which the initial reduction in size of the perfect wing takes place in Cenchreini and Derbini). The difference between the perfect, but small, wing (as in *Dysimia* or *Zeugma*) and the least modified "typically zoraidine" wing (as in *Pamendanga*) is far less than the difference in shape between the wing of *Pamendanga* and that of *Muiria*, or, to remain within Zoraidini, of *Diostrombus*. The writer accordingly feels unable, on present evidence, to accept the limit arbitrarily fixed by Muir between two steps in the above process (that is, between *Pamendanga* and *Zeugma*) as indicative of a fundamental division of the entire family. In this report, therefore, the family is regarded as falling merely into the six tribes currently recognised.

In Derbidae, all members of which are relatively highly specialised, the Cenchreini, as a group, most nearly approach the primitive cixiid-like form, while some genera (*Vekunta*, *Cedusa*) also exhibit an unspecialised tegminal venation, and a comparatively unspecialised head.

The Cenchreini are not only the least specialised of Derbidae, but also the most plastic. The tegmina may elongate (*Persis*); its membrane (or distal area) may become relatively long in relation to the proximal " corium " (*Neocenchrea*), or conversely, relatively short (*Cenchrea exquisita* Uhl.); or the tegmina may become rather wide in proportion to their length (*Patarella**). The clavus is normally closed apically and the common stalk of the united claval veins enters its apex. In a few Cenchreini, however, the clavus is narrowly open (some *Phaciocephalus*, *Herpis*) and the common anal vein enters a transverse veinlet distad of the level of the claval apex. The vertex, normally quadrangular, narrowing anteriorly and about as long as broad across its base, may be twice as broad as long (*Phrygia*, *Goneokarella**), or highly compressed (*Contigucephalus*, *Cenanges**). In some genera (*Cedusa*, *Lamenia*, *Zeugma*) a subantennal process is developed; in others (*Cenchrea*, *Neocenchrea*) the lateral carina and the lower margin of the pronotum on each side may be foliately elevated and curved cephalad to form a semicircular chamber in which the antennae are accommodated.

The transition from Cenchreini to Derbini is comparatively slight, and is well exhibited in *Dysimia*; that between Cenchreini and Otiocerini, at least as far as the condition of the claval apex and cubital venation is concerned, is indicated in *Herpis* in Cenchreini and *Cobacella**[1] in Otiocerini. Muir (1918: 234) drew attention to the similarities between *Symidia* (which he placed in Cenchreini) and zoraidine genera. The tegminal venation, though not so clearly derbine as in *Dysimia*, is nevertheless of derbine form, and in both genera there is a distinct approach to the zoraidine type of wing; indeed, the differences lie in marginal contour rather than in relative size or venation.

The transition from ancestors of cenchreine facies to forms resembling present Zoraidini may possibly not have occurred directly. But genera such as *Equirria*, *Phenice* and *Paraphenice* resemble the zoraidine *Diostrombus* very closely in tegminal venation, and *Pamendanga* in tegminal shape. A remarkable combination of cenchreine and zoraidine characters is found in *Zeugma*, discussed below. The highly specialised Sikaianini have unquestionably originated from less specialised ancestors similar to *Diostrombus*. Indeed, when the size of the gaps between certain groups of cenchreine genera (*Lamenia-Paraphenice*) is compared with that between Zoraidini and Sikaianini, the question arises whether Sikaianini would not better be considered as of subtribal status.

The affinities of the small and compact Rhotanini appear to lie with Otiocerini, though the tegminal venation is in some respects (e.g., apical-cell proportions, condition of claval apex) closer to that of Cenchreini.

In conformation of the genitalia the Derbidae show great uniformity.

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[1] An asterisk indicates a new genus described in this paper.

There is certainly nothing in these structures to support the concept of two major divisions in this family, comparable to the subfamilies Asiracinae and Delphacinae in Delphacidae.

It is interesting to note that in species of at least two genera of Otiocerini, *Vivaha* and *Megatropis*, the teeth along the distal margin of the second post-tarsal segment are reduced and only the spine at each angle remains. The steps by which this condition has been reached are clearly visible in series of other otiocerine genera, and accordingly the possession of a structure so alien to the cixiid group of families does not cast doubt on the accepted taxonomic position of these species.

Another unusual character of interest in the family is the elongate apical rostral joint of *Vinata* and *Archara*. In both its appearance is abrupt: the writer is unaware of any graded series leading from this condition to the short ring-like apical segment which is otherwise general throughout the family.

While *Archara* is unmistakably otiocerine and not isolated in its group (it is very near *Heronax*), *Vinata* is unique. Its affinities lie with Cenchreini, but it is far removed from any other living genus. The long cylindrical antennae are approached by those in *Patara*. The head otherwise is more like that of an achilid than of any derbid. The long pronotum, with its strongly tricarinate elevated disc, is without parallel in the family. *Cenchrea* and its allies, *Goneokarella* and *Phrygia*, have a tricarinate pronotal disc, but in no way matching that of *Vinata*. The tegminal venation also is of a very uncommon pattern in possessing a row of subapical cells, each of which is about as long as its apical counterpart. A hint of how this may have developed is offered by the condition in *Goneokarella*, where a series of more or less uniform subapical cells is developed. Muir (1923 : 228) pointed out that the genitalia of male *Vinata* are of unmistakable derbid pattern. Through the kind assistance of Dr. China the writer has been able to confirm this finding. The female genitalia agree generally with those of other derbid genera.

KEY TO TRIBES OF DERBIDAE.

(1) (2) Tegmina with clavus open, occasionally closed ; at least second cubital vein not reaching hind margin directly but curving into subapical transverse line of cross veins ; often, but not invariably, common claval vein extending through open claval apex to join subapical transverse lines. Frons usually strongly compressed laterally . . . . (3)

(2) (1) Tegmina with clavus closed, rarely open ; second cubital vein reaching hind margin directly, or meeting transverse veinlets more or less rectangulately, transverse veinlets usually reaching to hind margin. Frons narrow, usually not strongly compressed . . . . (9)

(3) (4) Wings not more than half as long as tegmina, usually narrow or reduced with stridulatory organ on reduced anal lobe . . . (5)

(4) (3) Wings more than half as long as tegmina, ampliate . . . . (7)

(5) (6) Eyes not reaching to base of clypeus ; tegmina with subcostal cell long . . . . **Zoraidini**

(6) (5) Eyes reaching to base of clypeus ; tegmina with subcostal cell short . . . . **Sikaianini**

(7) (8) Tegmina more than 2·5 times as long as broad, clavus open **Otiocerini**

(8) (7) Tegmina less than 2·5 times as long as broad, clavus closed, or nearly so . . . . **Rhotanini**
(9) (10) Tegmina with clavus not more than half as long as whole tegmen. M and Cu with not less than 8 branches at margin. Wings not more than half as long as tegmina . . . . **Derbini**
(10) (9) Clavus at least half as long as whole tegmen. M and Cu usually with less than 8 branches at margin. Wings more than half as long as tegmina . . . . **Cenchreini**

TRIBE ZORAIDINI.

Tegmina usually more than 3·5 times as long as broad; united claval veins prolonged into submarginal line of transverse veins in tegmina, or if not, then forming an even shallow curve with it. Wings at most scarcely exceeding half length of tegmina, often narrow; vein M simple or forked once, Cu_1 with not more than three branches at margin. Subantennal processes and pronotal carinae usually absent or very small.

The above revised definition permits the transfer of *Zeugma* from Derbini to Zoraidini. It has hitherto fallen into Derbini through the application of the single-character criterion, erected by Muir, of a "normally developed" or "reduced" anal area in the wing. The distinctive feature of *Zeugma* is merely the convexity of the apical margin of the wing; the venation is simple and not dissimilar from that of other zoraidine genera, such as *Helcita*. In Derbini the increase in branching of M and Cu_1 in the tegmen tends to be accompanied by an increase, though in less degree, of these veins in the wing. The complexity of the tegminal media is considerable in *Derbe*, *Zeugma* and zoraidine genera as currently recognised, but in the media of the wings the contrast between *Derbe* and all the others is very marked.

In Derbini the anterior veinlets of M at the margin of the tegmina conform to a definite pattern: the anterior two apical veinlets arise from a common stalk; the third is simple, while the fourth and fifth arise from a common stalk. In Zoraidini the fourth and fifth typically arise independently from the main stem of M. In this respect *Zeugma* agrees with the zoraidine condition.

The interesting New World *Symidia*, as Muir pointed out, resembles zoraidine genera in the proportionate length of wing to tegmina. To this might be added that the relation of the united claval veins to the submarginal line of cross veins is not unlike that in Zoraidini, while the wing venation and wing shape are close to that of *Zeugma*. The shape of the tegmina, however, and the branching of M are of derbine, not zoraidine, pattern.

Key to Genera of Zoraidini.

(1) (2) All median sectors single, generally six; antennae generally shorter than frons, ovate, clavate, or subclavate, arista apical; styles of ovipositor very short . . . . (3)
(2) (1) Media generally with five sectors, one furcate . . . . . . (13)
(3) (4) Basal median cell narrow, wings about half as long as tegmina, apex rounded . . . . (5)
(4) (3) Basal median cell wide and short; not more than three and a half times as long as broad, wings much less than half as long as tegmina, apex acute . . . . (11)
(5) (6) Head as wide as thorax or wider . . . . (7)

(6) (5) Head not as wide as thorax . . . . (9)

(7) (8) Apex of clavus not surpassing basal third of tegmina, anal veins present in wing . . . . **Zeugma** Westw.

(8) (7) Apex of clavus surpassing basal third of tegmina, wings without anal veins . . . . **Lydda** Westw.

(9) (10) Antennae much shorter than frons, subovoid . . **Proutista** Kirk.

(10) (9) Antennae as long as frons . . . . **Shizuka** Mats.

(11) (12) Tegmina about three times as long as broad ; cell Sc more than a quarter width of cell R ; mesonotum with three distinct carinae . . . . **Diostrombus** subg. **Camma** Dist.

(12) (11) Tegmina about four times as long as broad ; cell Sc obsolete or extremely narrow ; mesonotum with carinae obsolete or absent . . . . **Diostrombus** subg. **Diostrombus** Uhl.

(13) (14) Second or third median sector furcate . . . . (15)

(14) (13) First medial sector with two to four branches . . . . . (23)

(15) (16) Second medial sector furcate . . . . **Neocamma** Mel.

(16) (15) Third medial sector furcate . . . . (17)

(17) (18) Head in profile produced conically . . . . (19)

(18) (17) Head in profile not produced . . . . (21)

(19) (20) Vertex with carinae contiguous ; third antennal segment (arista) inserted definitely subterminally . **Helcita** subg. **Jada** Dist.

(20) (19) Vertex with carinae widely separated ; third antennal segment inserted on obliquely truncate apical margin. **Helcita** subgen. **Helcita** Stål

(21) (22) Base of clypeus in profile straight, antennae of female not with a pointed flange . . . . **Pamendanga** Dist.

(22) (21) Base of clypeus in profile curved, antennae of female with a pointed flange . . . . **Acanthocerana** Metc.

(23) (24) Antennae shorter than frons, arista inserted apically ; valvulae of ovipositor very short . . . . **Raizoda** Muir

(24) (23) Antennae generally longer than frons with arista inserted subapically ; valvulae of ovipositor not reduced, about twice as long as broad . . . . (25)

(25) (26) Head in profile conically produced . . . . **Pseudohelcita** Muir

(26) (25) Head in profile not conically produced . . . . (27)

(27) (28) Vertex quadrate, very much wider than long, frons as wide as an eye . . . . **Peggia** Kirk.

(28) (27) Vertex longer than wide or but little wider than long . . (29)

(29) (30) Frons not linear, carinae not contiguous, a sulcus down middle widening in distal half . . . . (31)

(30) (29) Frons more or less linear, carinae contiguous . . . . . . (35)

(31) (32) Basal median cell short, about three times as long as broad ; wings extremely short, broad, and strongly veined **Zoraidoïdes** Dist.

(32) (31) Basal median cell long and comparatively narrow, wings half as long as tegmina . . . . (33)

(33) (34) Cu_1 forked distad of claval apex, Cu_{1a} two-branched ; cell Sc + R separated from apical margin by two rows of cells, subapical long, apical very short ; clypeal disc at widest equal to width of frons. Antennal arista markedly subapical **Teutberga** Jac.

(34) (33) Cu_1 forked almost level with union of claval veins, Cu_{1a} simple ; cell Sc+R separated from apical margin by a single row of

long cells; clypeal disc at broadest part twice as wide as frons; arista apparently apical . . . . **Shirakiana** Metc.

(35) (36) Posterior margin of tegmina undulate; basal medial cell about three times as long as broad, comparatively broad distally **Losbañosia** Muir

(36) (35) Posterior margin of tegmina not undulate . . . . (37)

(37) (38) Apical segment of rostrum short and expanded at apex, disc-like . . . . **Monochorhynchus** Muir

(38) (37) Apical segment of rostrum not as above . . . . (39)

(39) (40) Hind margin of pronotum straight, or nearly so **Neodiostrombus** Muir

(40) (39) Hind margin of pronotum excavate . . . . (41)

(41) (42) Costal margin produced on basal quarter . . . . **Peggia** Kirk.

(42) (41) Costal margin not produced . . . . (43)

(43) (44) First medial sector with four branches **Zoraida** subgen. **Neozoraida** Muir

(44) (43) First medial sector with two branches . . . . (45)

(45) (46) Antennae cylindrical or only slightly flattened **Zoraida** subgen. **Zoraida** Kirk.

(46) (45) Antennae broad and flattened . . **Zoraida** subgen. **Peggiopsis** Muir

Zoraida Kirkaldy.

Subgenus *Peggiopsis* Muir.

Peggiopsis Muir, 1913 : 72. Orthotype, *Peggiopsis rufa* Muir, *loc. cit.*

Zoraida (*Peggiopsis*) *wallacei* Muir.

Muir, 1918 : 206.

The writer has seen Muir's manuscript description of the above species. It was originally headed "*Zoraida singaporensis* sp. n.," but the trivial epithet was subsequently deleted and "*wallacei*" written above it. The alteration was not made in the synoptical table (*ibid.* : 175), where "*singaporensis*" appears as a *nomen nudum.*

Peggia Kirkaldy

Kirkaldy, 1901 : 6. Orthotype, [*Nebrissa*] *nitida* Stål, 1870 : 751.

Peggia kawandana sp. n. (fig. 1A–F).

Male: length, 4·8 mm.; tegmen, 14·3 mm.

Rostrum with apical joint suborbicular. Post-tibiae unispinose laterally and with five spines apically, one separated from the remainder; basal metatarsal joint with five spines, second metatarsal joint five-toothed.

Fuscous; all carinae, legs, and lower surface of thorax ivory to stramineous. Antennae pale with a linear suffusion along middle of each face. Tegmina hyaline, veins basally ivory-yellow, distally brown.

Anal segment elongate, porrect caudad, flat, acute at apex, anal foramen at basal quarter. Pygofer bilaterally symmetrical, laterodorsal angles produced in a slightly curved subspinose process, medioventral process triangular. Aedeagus tubular, shallowly spirally grooved in basal portion, flagellum minutely denticulate on right side, the denticulate portion ending in a short blunt point ventrolaterad of remainder of flagellum; two lobes at apex, of subequal length, that on right side broad, compressed, with margin evenly rounded, that on left narrower and subtectiform. Genital styles long and narrow, curving laterad then mesodorsad, practically meeting in middle line at apex, a cornice-like ledge, convex above and concave below, on inner face near base.

Holotype, ♂, UGANDA: Kawanda, 21.x.1939 (*H. Hargreaves*).

This is the second species to be described in this genus. It differs from the Philippine *P. nitida* in having a linear frons, a rostrum which does not surpass the post-trochanters, and in minor details of the tegminal venation. In *Peggia nitida* the frons is broad and the rostrum surpasses the post-trochanters. The writer believes that these differences are of subgeneric degree, and accordingly proposes a new subgenus, *Stenopeggia*, for the reception of *P. kawandana* Fennah, its typical subspecies.

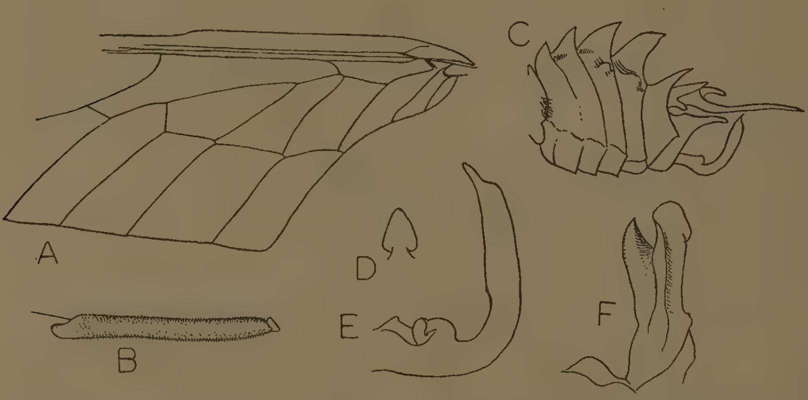

FIG. 1.—*Peggia kawandana* sp. n. A, basal part of tegmen; B, second antennal segment; C, abdomen, side view; D, medioventral process of pygofer; E, genital style, side view; F, aedeagus, dorsal view of apical portion.

Key to Genera of Sikaianini.

(1) (2) Cubital vein united in a common stem with media for some distance from base . . . . **Distantinia** Muir
(2) (1) Cubitus arising independently from base of tegmen, basal median cell present . . . . (3)
(3) (4) Basal median cell very narrow, reaching approximately to middle of tegmen . . . . **Leomelicharia** Muir
(4) (3) Basal median cell broad and short, not nearly reaching to middle of tegmen . . . . (5)
(5) (6) Antennae as long as head and thorax combined, or nearly so **Muiria** Kirk.
(6) (5) Antennae not as above . . . . (7)
(7) (8) Antennae about as long as frons; wings one-third of length of tegmina . . . . **Sikaiana** Dist.
(8) (7) Antennae longer than frons; wings less than one-eighth of length of tegmina . . . . **Mula** Ball

Tribe Sikaianini.

Mula Ball.

Ball, 1928 : 198. Orthotype, *Mula resonans* Ball, *ibid.*

Mula thrinacis sp. n. (fig. 2A–E).

Male : length, 2·0 mm. ; tegmen, 5·8 mm. *Female :* length, 1·8 mm. ; tegmen, 5·2 mm.

Lateral carinae of vertex and frons contiguous, diverging only at extreme base of vertex to form with basal line a small equilateral triangle ; eyes reaching clypeal suture ; antennae cylindrical, simple, evenly studded with rather widely spaced sensory pits, narrowed before apex and with arista situated dorsally. Clypeus broader than long in middle line ; rostrum extremely short, almost sessile. Post-tibiae with ten small uneven spines at apical margin ; basal metatarsal joint six-spined at apical margin, second metatarsal joint with four spines (2 + 2). Tegmina with costal margin beset with 33 secretory pustules in an even row in basal half ; costal cell narrow, of subequal width throughout, traversed by six short oblique veinlets, more or less evenly spaced and beginning two-fifths from base ; Sc with 6 branches at apex, R with four. Wings greatly reduced, bilobate, the smaller lobe bearing a striate sub-marginal area.

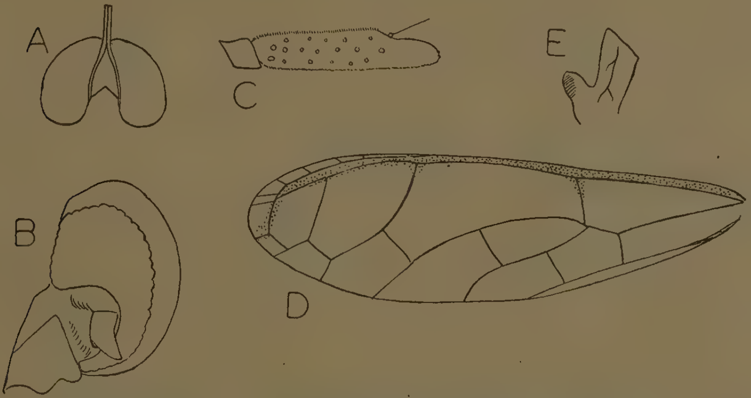

Fig. 2.—*Mula thrinacis* sp. n. A, head, dorsal view ; B, head in profile, antenna omitted ; C, antenna ; D, tegmen ; E, wing.

Ivory, powdered white ; profemora at apex, protibiae in basal half and at apex lightly suffused orange ; sclerite at apex of rostrum and post-tibial spines black ; eyes dark mauve-brown. Tegmina hyaline, veinlets entering costal margin, a small area at base of costal cell, Sc + R and main stem of M, orange-red ; the narrow cell Sc + R and the basal M-Cu crossveins at sides, infuscate.

Anal segment of male moderately short, somewhat decurved distally, anal style strongly decurved. Pygofer with laterodorsal angles strongly produced in a stout process, acute at apex. Aedeagus tubular, a slight eminence in middle of dorsal margin, flagellum laterally compressed, of approximately equal width throughout, abruptly tapering to subacute apex, a stout chelate process on right side. Genital styles as figured, with a simple obliquely-tapering vertical process in the middle of dorsal margin.

Holotype, ♂, B.W.I. : St. Lucia ; Canelles, 27.xi.1935, " on leaves of *Thrinax* palm " (*H. E. Box*). Paratypes, 2 ♂, 1 ♀, same particulars as holotype.

This species differs from *M. resonans* Ball in tegminal coloration. *Mula* differs from *Muiria* and *Sikaiana* in tegminal venation, and from the latter in possessing very much smaller wings (which in *S. hyalinata*, the type species, are about half as long as the tegmina) and three extra spines at the apex of the post-tibiae.

Euklastus Metcalf, the only other New-world representative of this tribe, cannot, on present evidence, be separated from *Sikaiana*, as both the original diagnosis and figures of *E. harti* Metcalf, and the supplementary data (1938 : 305), agree well with the holotype of *Sikaiana hyalinata*. The distribution of this tribe as so far known embraces the East Indies (7 species), Northern Australia (2 species), West Africa (2 species), Seychelles (1 species), Philippines (8 species), Fiji (2 species), eastern U.S.A. (2 species) and Lesser Antilles (1 species).

TRIBE DERBINI.

Frons narrow, usually not strongly compressed. Tegmina relatively elongate, subtriangular, broadest slightly distad of middle, apical margin long and oblique ; clavus closed, rarely open, not extending for more than half of total length of tegmen ; M and Cu together with not less than eight veins at margin ; second cubital vein reaching hind margin directly, or meeting transverse veinlets more or less rectangulately, transverse veinlets usually reaching to sutural margin.

Wings not more than half as long as tegmina.

When at rest, members of this tribe carry the tegmina and wings spread out laterally at right angles to the axial line of the body, and tilted slightly obliquely upward.

Muir separated his concept Derbini from Cenchreini and Rhotanini by the number of apical branches of the first cubital vein in the tegmina, the first, in contrast to the others, having not less than four. By this definition he was compelled to place *Symidia* and *Dysimia* in the Cenchreini.

The writer, however, considers that their affinities lie with *Mysidia* and *Pseudomysidia* ; it is evident, moreover, that they are not at all closely related to any known cenchreine genus.

The revised definition of Derbini given above permits the transfer of *Symidia* and *Dysimia* to this tribe. They may be separated from other genera by characters given in the extended form of Muir's key which follows.

Mysidia elatior Fowler is otiocerine, and *Mysidia ? spreta* Fowler cenchreine : both are discussed under their respective tribes.

Key to Genera of Derbini.

(1) (2) Cu_1 in tegmina with four or more veins reaching hind margin . . (3)
(2) (1) Cu_1 with two or three veins reaching hind margin (excluding cross vein from Cu_{1b} to apex of clavus) . . . . (5)
(3) (4) Cu_1 with four veins reaching hind margin, the second vein forked once ; valvulae of ovipositor short and small . . **Mysidia** Westw.
(4) (3) Cu_1 with six or more veins reaching hind margin, the second vein not forked, valvulae of ovipositor long and large . . . . **Derbe** F.
(5) (6) Cu_1 with three branches reaching margin, pronotal lateral carinae only feebly indicated, lateral margin not upturned . . . . (7)
(6) (5) Cu_1 two-branched ; pronotal lateral carinae foliate, ventral lateral margin upcurved to form antennal fovea . . . . **Symidia** Muir

(7) (8) Media with seven branches at margin; common stalk of united claval veins much longer than separate portion of anterior claval vein; oblique portion of apical margin distinctly shorter than commissural margin . . . . **Dysimia** Muir

(8) (7) Media with not less than ten branches at margin; common stalk of united claval veins distinctly shorter than separate portion of anterior claval vein; oblique portion of apical margin as long as commissural margin . . . . **Pseudomysidia** Metc.

Derbe Fabricius

Fabricius 1803: 80. Logotype, *Derbe haemorrhoidalis* Westwood 1840: 82.

Derbe bergrothi Muir (fig. 3A).

Muir, 1923: 67.

The genitalia of the holotype are figured.

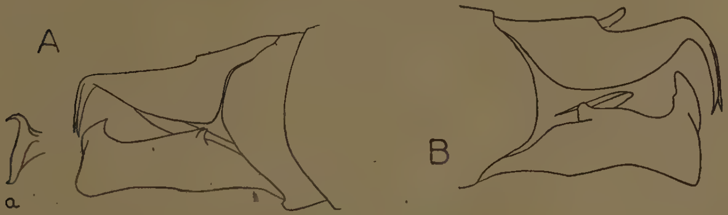

FIG. 3.—A, *Derbe bergrothi* Muir. Male genitalia in profile; (*a*) apex of genital style, posterior view. B, *Derbe longitudinalis* Dist. Male genitalia in profile.

Derbe championi Muir (fig. 4A, B).

Muir, 1918: 230.

The figures are of the holotype.

Derbe longitudinalis Distant (fig. 3B).

Distant, 1907: 395.

The figure is based on a male in the type series.

Derbe substrigilis Westwood (fig. 4C, D).

Westwood, 1851: 209.

The figures are based on a female specimen determined by Westwood.

Derbe strigipennis Westwood.

Westwood, 1840: 83.

Anal segment of holotype female short with latero-apical angles produced in a pair of finger-like lobes, each shorter than remainder of anal segment. Posterior margin of pregenital sternite produced medially in an almost square lobe, with parallel sides and truncate apex.

Derbe semistriata Westwood.

Westwood, 1840 : 83.

Head as in *D. strigipennis*. Tegmina clear, with dark veins ; apical cells of M slightly suffused with brown ; cells of corium each with middle portion darker brown than near margins. The veins in the type are darker than in *D. strigipennis*.

The type material in the Hope Collection consists of a single specimen devoid of the abdomen.

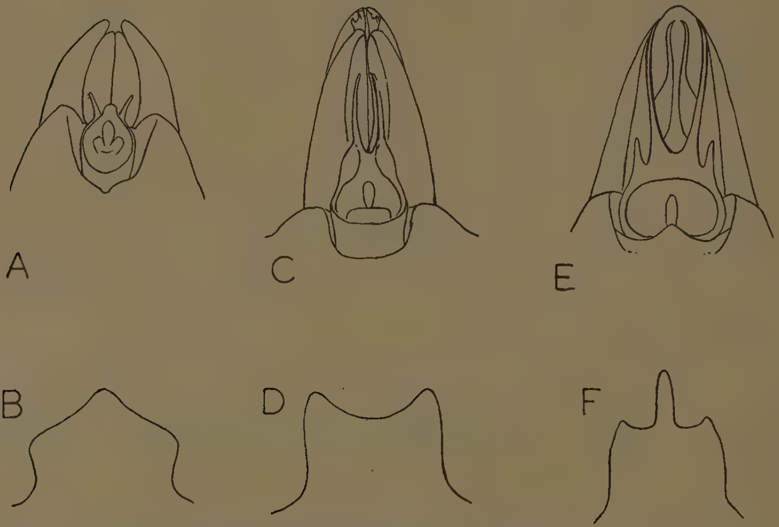

Fig. 4.—a, *Derbe championi* Muir. Anal segment and female genitalia, dorsal view ; b, posterior margin of seventh abdominal sternite.
c, *Derbe substrigilis* Westw. Anal segment and female genitalia, dorsal view ; d, posterior margin of seventh abdominal sternite.
e, *Derbe westwoodi* Fowl. Anal segment and female genitalia, dorsal view ; f, posterior margin of seventh abdominal sternite.

Derbe westwoodi Fowler (fig. 4e, f).

Fowler, 1900 : 71, pl. 8, fig. 16, 16*a*.
Derbe currani Metcalf, 1938 : 309, pl. 19.
Derbe uliginosa Fennah, 1945 : 436.

Venezuela : E. Carabobo, Las Trincheras, 1.vii.1950 (*F. Fernandez Yepez*) One male. The genitalia of a female in the restricted type series (*vide* Muir, 1918 : 230) are figured. The venation near the base of the first medial sector is rather variable, even between the tegmina of a single specimen, and cannot be relied upon as a criterion of specific difference. The Trinidad material of *D. uliginosa* differs from the Venezuelan in that the veins are brown rather than fuscous-piceous, while the clear parts of the cells instead of being colourless are faintly suffused with brown. Moreover the stigmal area is mainly translucent-yellow, whereas in the Venezuelan material the distal veinlets of Sc are yellow but the intervening cells are fuscous. On the basis of these differences the Trinidad population is here recognised as a geographical subspecies, *D. westwoodi uliginosa* Fennah.

B.W.I.: Trinidad, Carapo, 5.ix.1949 (*R. G. Fennah*). 1 ♀.

Derbe rubigosa sp. n. (fig. 5A–D).

Male: length, 7·1 mm.; tegmen, 14·0 mm.

Vertex viewed from above, slightly longer than broad; frons narrow, with disc concave, in profile almost symmetrically convex, with genae broadest at middle; antennae large, first joint attached to side of second joint, so that it is overlapped by base of second joint; second joint inflated, expanding distad, not reaching beyond middle of eyes; maximum width distinctly exceeding half length of eye.

Fuscous; lower half of genae, and of second antennal joint, lateral fields of pronotum and coxae light brown. Posterior margin of mesonotum and posterolateral areas of third to sixth abdominal tergites sordid yellow. Tegmina hyaline with faint brown suffusion; costal cell, subcostal vein including veinlets at apex, M_{1+2} just basad of their fork, M_1 (except for two interruptions) including apical veinlets dull yellowish-brown, veins otherwise fuscous; two longitudinal bars in cell Sc + R, and one medial bar in each other principal cell of corium, and a spot overlying apex of clavus and extending across posterior vein of Cu_1 fuscous; fork of M_{1+2} and all veins bounding subapical cells of M and Cu slightly overlain with brown; apical cells of M and Cu faintly infuscate in two large rounded patches, both adjoining margin. Wings hyaline, suffused with fuscous at apex, veins fusco-piceous.

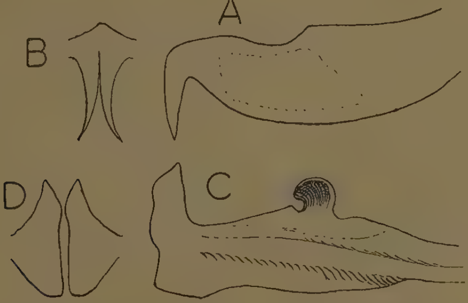

FIG. 5.—*Derbe rubigosa* sp. n. A, anal segment of male, side view; B, do., posterior view; C, genital style, side view; D, posterior view of apical portion of genital styles.

Anal segment of male in profile with ventral margin only shallowly convex, produced distally in a pair of rather long processes, relatively slender and tapering distally, deflexed almost through 90°. Pygofer with lateral margins convex. Genital styles in profile moderately broad, mediodorsal process thin, broad, falcate and hollowed, with a notch in the margin at its base. Apical processes in posterior view triangular with inner margin almost straight, and ventral and distal margins almost parallel.

Holotype, ♂, VENEZUELA: Aragua, Rancho Grande, ix.1949 (*Rácenis*).

This species is distinguished by the shape of the genitalia, in which it is nearest to *D. longitudinalis* Dist. The frons is markedly narrower than in

D. westwoodi, in which, though the lateral margins are raised, the disc is flattened rather than concave; moreover the profile of the frons is more deeply rounded in its middle portion. The tumescence of the second antennal joint of the male appears to be without parallel in the genus: a similar development—so far known only in one species—occurs in the otiocerine *Flaccia* (*F. oediceras* Fenn.)

Mysidia Westwood.

Mysidia, Westwood, 1840: 84. Logotype, *Derbe pallida* Westwood 1841: 477.

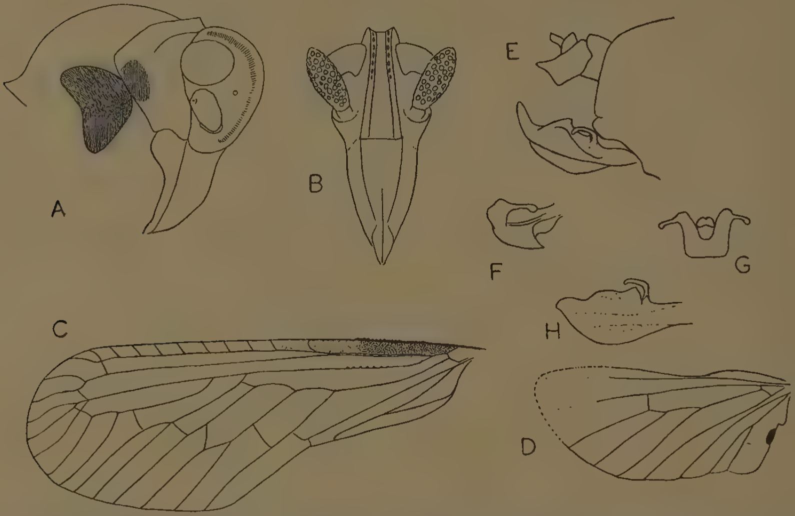

Fig. 6.—*Mysidia costata* (F.). A, Head, pronotum, mesonotum and tegula, side view; B, head, anterior view; C, tegmen; D, wing; E, anal segment, pygofer and right genital style, side view; F, apical portion of aedeagus, side view; G, apical portion of aedeagus, posterior view; H, right genital style, side view.

Mysidia costata (Fabricius) (fig. 6A–H).

Derbe costata Fabricius, 1803: 81.

Male: length 4·5 mm.; tegmen, 10·5 mm.

Second segment of antennae about 2·7 times as long as wide in middle, length slightly exceeding diameter of eye.

Pallid greyish-white; a round spot on lateral fields of pronotum, and tegulae, piceous. Tegmina transparent; powdered white. Costal cell and distal transverse veins narrowly pale fuscous.

Anal segment short, subquadrate in profile and deflexed through 40°. Pygofer with lateral margin convex, with an incision at middle. Genital styles with ventral margin convex, dorsal margin sinuate; a finger-like process curved through 120° one-third from base, followed distally by a small broad triangular eminence, distad of which margin is angulately convex; apex of style directed upward and mesad. Aedeagus bilaterally symmetrical, short, tubular, in profile almost fan-shaped with dorsal margin shallowly concave; ventral margin deeply concave basally, convex distally, apex obliquely truncate; a short knobbed process arising dorsally at apex, directed anteriorly and outward. Apical dorsal margin of phallobase slightly excavate in middle line.

Redescribed from B.W.I.: Trinidad; Verdant Vale, 1920, 1 ♂ (*F. W. Urich*). The genitalia are figured for comparison with material from other localities.

Mysidia lactiflora Westwood (fig. 7B).

Westwood, 1840 : 83.

Frons at apex not wide, clypeus with median carina distinct, lateral carinae feeble: antennae about as long as frons.

Posterior margin of subgenital plate convex, incised medially.

In the female type from Brazil the anal segment has been destroyed.

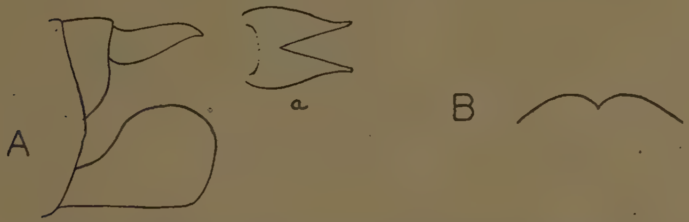

FIG. 7.—A, *Mysidia albipennis* Westw. Anal segment, pygofer and left genital style, side view; (*a*) lateroapical angles of anal segment, dorsal view.
B, *Mysidia lactiflora* Westw. Posterior margin of pregenital sternite.

Mysidia albipennis Westwood (fig. 7A).

Westwood, 1840 : 83.

Clypeus relatively wide with rounded sides, with median carina distinct and lateral carinae obsolete or only represented basally. Pronotum with a black spot on each side.

The type is a male from Vera Cruz.

Pseudomysidia Metcalf.

Metcalf, 1938 : 317. Orthotype, *Pseudomysidia fuscovaria* Metcalf.

Pseudomysidia fuscovaria Metcalf.

Metcalf, 1938, *loc. cit.*

Pseudomysidia fuscovaria araguana subsp. n. (fig. 8A).

Female: length, 3·0 mm.; tegmen, 6·1 mm.

Stramineous, powdered white. Tegmina translucent, powdered white, marked with fuscous as figured. Wings transparent, powdered white.

Pregenital sternite produced caudad in a broad deeply rounded lobe.

Holotype, ♀, Venezuela: Aragua, Rancho Grande (no date) (*Rácenis*).

This specimen differs from the type in having one fewer sector in M in both tegmina, and in the infuscation of the clavus. It may prove to be specifically distinct when males can be compared.

Dysimia Muir.

Muir, 1924: 462. Orthotype, *Dysimia maculata* Muir, *ibid*: 463.

Dysimia fuscoclypeata sp. n. (figs. 8B–D, 9A–C).

Female: length, 2·1 mm.; tegmen, 5·0 mm.

Generally similar to *D. maculata* Muir.

Stramineous; powdered white. Two spots on genae before eyes, clypeus except in middle distally, a spot on pronotum behind eyes, meso-pleurites in part, fuscous. Tegmina and wings marked generally as in *D. maculata*, but apical cells of former not at all infuscate. Transverse veins in wings fuscous.

Pregenital sternite produced caudad in a broad lobe with its sides only slightly convergent distally and the apex shallowly rounded-truncate.

Holotype, ♀, Venezuela: Aragua, Rancho Grande, 1100m., 1.x.1950 (*F. Fernandez Yepez*).

Paratype, 1 ♀, Aragua, Camino Choroni, 24.iii.1949 (*H. E. Box*)

This species differs from the Puerto Rican *D. maculata* in the infuscate clypeus and mesopleurites, and in the total absence of infuscation on tegulae, mesonotum and abdomen. In the tegmina the apical cells are not at all infuscate, and of the veins only the transverse series is suffused.

The pregenital sternite of the female differs widely in shape from that of *D. maculata*.

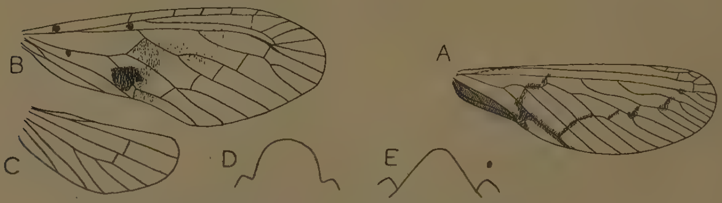

Fig. 8.—A, *Pseudomysidia fuscovaria araguana* subsp. n. Tegmen.
B–D, *Dysimia fuscoclypeata* sp. n. B, tegmen; C, wing; D, posterior margin of pregenital sternite.
E, *Dysimia putilla* sp. n. Posterior margin of pregenital sternite.

Dysimia putilla sp. n. (fig. 8E).

Female: length, 2·2 mm.; tegmen, 4·3 mm.

Closely similar to *D. maculata* in form and coloration. Basal portion of frons, excluding the secretory pits, a single narrow stripe on side of head before eyes, a minute spot on genae above base of antennae, dark fuscous. A broad area on lateral lobes of pronotum, posterior margin of tegulae, and a slight suffusion on mesonotum light sepia-brown to fuscous; abdomen with third segment sublaterally, fourth prominently laterally and with four short antero-posterior stripes between them, fifth with four paler spots, and sixth with two pale submedian spots and two spots laterally, fuscous.

Tegmina with a small spot on Sc + R + M fork, a broad and faint suffusion in costal cell at base of Sc + R fork, a round and distinct spot overlying M just basad of first sector, and a crescentic spot overlying base of first three apical veinlets of M. Veins interruptedly and diffusedly overlain with fuscous.

Pregenital sternite produced caudad in a subequilaterally triangular lobe with the apex shortly truncate.

Holotype, ♀, B.W.I.: St. Lucia, Quilesse, 22.ii.1941, " 1000 ft., in mountain forest " (*R. G. Fennah*).

This species is close to *D. maculata*, but differs appreciably in markings and in the shape of the pregenital sternite of the female. On the basis of the specimens before the writer it is evident that a lateral marginal carina is developed on each side of the pronotum. This is fine for the posterior two-thirds of its length, but, after an interruption, thickened and more elevated anteriorly. Muir's figure (1924 : 470) omits a transverse vein in the tegmen between Cu$_1$ fork and Cu$_{1b}$, and another between Cu$_{1b}$ and the margin just distad of the claval apex.

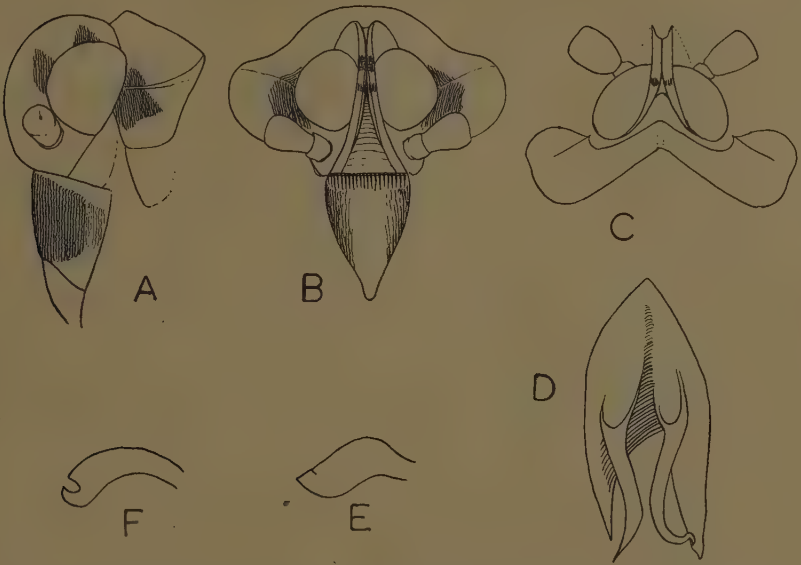

Fig. 9.—*Dysimia fuscoclypeata* sp. n. A, Head in profile ; B, head and pronotum, anterior view ; C, head and pronotum, dorsal view.

Symidia flava Muir. D, dorsal view of aedeagal flagellum, upper end of figure distad, lower basad ; E, lower lobe of flagellum, left side, side view ; F, upper lobe of flagellum, left side, side view.

D. putilla differs from *D. fuscoclypeata* in having the clypeus entirely pallid, and the tegmina and abdomen maculate. In the tegmina there is no marking in *fuscoclypeata* corresponding to the crescentic spot in *putilla*, and the veins in *fuscoclypeata* are not overlain with an interrupted fuscous suffusion.

For the sake of distributional record the writer notes here an observation of "swarming" *Dysimia* sp. on the underside of cacao leaves, Mt. Horne Estate, Grenada, B.W.I. (Sept. 1947). The tegmina and wings, as in *Derbe* and *Mysidia*, are held outspread and sloping upward when the insect is at rest.

Symidia.

Muir, 1918 : 234. Orthotype, *Symidia flava* Muir.

Symidia flava Muir (fig. 9D–F).

Muir, 1918, *loc. cit.*

Flagellum with four lobes, the lower pair in profile about twice as broad as upper pair, and bluntly pointed at apex; upper lobes decurved distally and falcate at apex, the right lobe a little broader at apex than left lobe.

Two males and a female, B.W.I.: Trinidad, Mt. Harris (*C. L. Withycombe*). This is probably the geographical representative of *flava*, the type of which is from British Guiana.

TRIBE CENCHREINI.

Frons moderately narrow, rarely broad, occasionally strongly laterally compressed. Tegmina of variable proportions, at least 2·5 times as long as broad but never exceptionally long; apical margin rounded, moderately short, rarely extended and oblique; M and Cu with less than eight branches at margin; clavus closed, rarely narrowly open, extending for at least half of total length of tegmen; second cubital vein reaching hind margin directly or meeting transverse veinlets more or less rectangulately, transverse veinlets reaching to hind margin. Wings more than half as long as tegmina.

Several well-marked generic groups can be recognised (e.g., *Lamenia* group, *Phenice* group, *Cenchrea* group, *Phaciocephalus* group) and, with sufficient material, it may prove possible to develop a natural sub-tribal classification.

According to the definition given above *Symidia* and *Dysimia* are excluded from this tribe.

The Old World genera are not treated critically here; opportunity is taken to revise the species-groups of America which in the past have been referred to *Phaciocephalus* (*sensu lato*). Caldwell (1944 : 100) has already recognised three groups, defined principally by male genitalic characters: one of these groups is *Omolicna*, and two others are named below.

Key to Genera of Cenchreini.

(1) (2) Subantennal process well developed . . . . (3)
(2) (1) Subantennal process absent or very small . . . . . . (25)
(3) (4) Lateral pronotal carinae and ventral lateral margins of pronotum not subfoliately raised to form a cup-like antennal fovea . . . . (5)
(4) (3) Lateral pronotal carinae and lateral margins foliate, forming a deeply concave fovea . . . . (21)
(5) (6) Tegmina with subcostal cell long . . . . (7)
(6) (5) Tegmina with subcostal cell short . . . . (17)
(7) (8) Frons with a median carina . . . . **Eocenchrea Muir**
(8) (7) Frons without a median carina . . . . (9)
(9) (10) Vertex transverse, much broader than long . . . . . . (11)

(10) (9) Vertex not or very little broader than long . . . . (13)

(11) (12) Sc + R fork about level with, and Cu$_1$ fork much distad of, union of claval veins . . . . **Malenia** Haupt

(12) (11) Sc + R fork basad of, and Cu$_1$ fork level with, union of claval veins . . . . **Cedusa** Fowler

(13) (14) Frontal carinae not contiguous; tegmina with Sc + R fork almost level with union of claval veins; Cu$_{1b}$ ending at transverse vein . . . . (15)

(14) (13) Frontal carinae contiguous; tegmina with Sc + R fork and Cu$_1$ fork far distad of level of union of claval veins; Cu$_{1b}$ reaching margin . . . . **Dawnarioides** Dozier

(15) (16) Vertex narrow, acutely excavate posteriorly; pronotum much shorter in middle than at sides . . . . . . **Paraphenice** Muir

(16) (15) Vertex trapezoidal, shallowly excavate posteriorly; pronotum almost as long in middle as at sides . . . . **Fescennia** Stål

(17) (18) Apex of head angulate in profile; subantennal process forming a ridge below antennae . . . . (19)

(18) (17) Vertex curving into frons; profile not angulate; subantennal process semicircular, antennae ovate, not reaching to apex of head . . . . **Cyclometopum** Muir

(19) (20) Antennae small . . . . **Lamenia** Stål

(20) (19) Antennae broad, as long as frons . . . . **Neolamenia** Muir

(21) (22) Frons very narrow, lateral carinae contiguous to near apex **Fordicidia** Dist.

(22) (21) Frons narrow but lateral carinae not touching . . . . . . (23)

(23) (24) Vertex declivous, curving into frons; frons in profile weakly convex; genae narrow; M with four sectors, the distad forked at transverse line . . . . **Neocyklokara** Muir

(24) (23) Vertex horizontal, meeting frons in an angle; frons in profile strongly convex; genae broad; M with five sectors, the distad forked basad of transverse line . . . **Muirileguatia** Metc.

(25) (26) Lateral pronotal carinae and ventral lateral margins of pronotum not foliately raised . . . . (27)

(26) (25) Lateral pronotal carinae and ventral margins of pronotum foliate, forming an antennal fovea . . . . (51)

(27) (28) Head distinctly angulate in profile . . . . (29)

(28) (27) Head rounded in profile, vertex curving into frons . . . . . (41)

(29) (30) Subcostal cell long . . . . (31)

(30) (29) Subcostal cell short . . . . (35)

(31) (32) Vertex markedly produced before eyes, acutely angulate in profile . . . . **Persis** Stål subgen. **Persis**

(32) (31) Vertex not produced, forming with frons an obtuse angle in profile . . . . (33)

(33) (34) Head with a small subantennal process; tegmina not three times as long as broad; Sc + R fork at basal quarter; no Sc + R + M stalk, M$_3$ and M$_4$ not united . . . . . . **Goneokara** Muir

(34) (33) Head without a subantennal process; tegmina fully three times as long as broad; a distinct Sc + R + M stalk; Sc + R fork at least distad of basal third, M$_3$ and M$_4$ united in a common stalk as far as subapical cross-veins **Persis** Stål subgen. **Eritalaena***

(35) (36) Pronotum with a distinct medial disc bounded laterally by carinae . . . . (37)

(36) (35) Pronotum with no distinct medial disc . . . . (39)

(37) (38) Frons little longer than broad, margins convex ; antennae long, apical joint of rostrum long . . . . **Vinata** Dist.

(38) (37) Frons distinctly longer than broad, margins parallel ; antennae very short, apical joint of rostrum short . . . **Goneokarella***

(39) (40) Tegmina with each sector of M forked once at about same level **Vekunta** Dist.

(40) (39) Tegmina with anterior sector of M three-branched distally, posterior sector simple . . . . **Perandenina** Dist.

(41) (42) Antennae large, at least in female, reaching beyond apex of head . . . . (43)

(42) (41) Antennae small, not surpassing apex of head . . . . . . (47)

(43) (44) Frons linear ; carinae contiguous to near apex ; vertex small, triangular ; M forked level with or distad of apex of clavus (45)

(44) (43) Frons narrow but not linear ; carinae not contiguous ; M forked distinctly basad of level of apex of clavus . . . . **Equirria** Dist.

(45) (46) Tegmina with Cu forked basad of level of apex of clavus **Aequalicum** Dist.

(46) (45) Tegmina with Cu forked distad of level of apex of clavus **Patara** Westw.

(47) (48) Sc + R forked level with union of claval veins ; M with first sector forked level with apex of clavus . . . . (49)

(48) (47) Sc + R forked distad of union of claval veins . . **Dawnaria** Dist.

(49) (50) Head not laterally compressed, frons broad ; tegmina less than three times as long as broad . . . . **Phrygia** Stål

(50) (49) Head laterally compressed, frons narrow ; tegmina more than three times as long as broad . . . . **Phenice** Westw.

(51) (52) Disc of frons moderately broad, usually medially carinate, flat or slightly convex, not at all concave . . . . (53)

(52) (51) Frons not as above . . . . (55)

(53) (54) Vertex nearly twice as broad as long in middle ; frons broad, lateral margins parallel ; genital styles narrowed at base ; medioventral process elongate-conical ; pregenital sternite produced caudad in a quadrate lobe, narrowing distally and apically transverse . . . . **Oropuna***

(54) (53) Vertex as long as broad or longer than broad ; frons usually medially carinate ; genital styles broadened at base, medioventral process triangular ; pregenital sternite produced caudad in a subcircular lobe . . . . **Herpis** Stål

(55) (56) Tegmina with subcostal cell short (not extending basad of claval apex) ; frons very narrow ; a fine transverse carina between vertex and frons ; pronotum with a distinct medial disc bounded by carinae . . . . (57)

(56) (55) Tegmina with subcostal cell long, no demarcated pronotal disc (59)

(57) (58) Medioventral process present on pygofer . . . . **Cenchrea** Westw.

(58) (57) Medioventral process reduced . . . . . **Contigucephalus** Caldw.

(59) (60) Tegmina with Sc + R fork distad of Cu_1 fork, latter about level with union of claval veins . . . . (61)

(60) (59) Tegmina with Sc + R fork basad of Cu_1 fork, latter about level with claval apex . . . . (63)

(61) (62) Tegmina with papillate portion of anterior margin equal to smooth basal portion (node medial) ; pygofer with no medioventral process . . . . **Neocenchrea** Metc.

(62) (61) Tegmina with papillate portion of anterior margin distinctly shorter than smooth basal portion (node distad of middle) ; pygofer with a medioventral process **Persis** Stål subgen. **Anapersis***

(63) (64) Apex of clavus distad of middle of tegmen . . . . (67)

(64) (63) Apex of clavus at middle of tegmen ; head compressed, but not linear ; frons widest at distal border . . . . (65)

(65) (66) Pronotum medially carinate, with a median discal area ; apical cells of M in tegmina not more than twice as broad as long ; lateral margins of vertex not foliate and curved outward basad . . . . **Basileocephalus** Kirk.

(66) (65) Pronotum with an elevated disc bounded by sinuate carinae, median carina weak . . . . **Cenanges***

(67) (68) Frons in middle line at least three times as long as broad at widest part. Anal segment of male very long and narrow **Anchimothon***

(68) (67) Frons relatively shorter ; anal segment of male not as above . (69)

(69) (70) Frons in middle line more than twice as long as broad at widest part, tegmina with first M fork basad of claval apex **Phaciocephalus** Kirk.

(70) (69) Frons in middle line less than twice as long as broad at widest part, tegmina with first M fork at level of claval apex **Omolicna** Fenn.

Cenchrea Westwood.

Cenchrea Westwood, 1841 : 15. Haplotype, *Cenchrea dorsalis* Westwood.

This genus is one of a small natural group in which the frons is more or less narrowed, and separated from the vertex by a fine transverse carina, the Sc + R fork is usually distad of the level of the claval apex (" subcostal cell short "), though not invariably, and the median discal area of the pronotum is elevated and very distinctly tricarinate or only the median carina feeble. The other genera which share these characters are *Contigucephalus* Caldwell and *Cenanges* (described below).

Cenchrea itself is at present unequally divided. A striking feature of its species is the exuberant development of processes on the lateral margins of the pygofer and on the genital styles. *C. dorsalis* stands strongly apart from the other species, *C. exquisita* and others described below. These latter form a compact natural group extending in a chain from British Guiana through Venezuela and Trinidad to Grenada and St. Vincent, but not further northward. Apart from their bold tegminal markings they are characterised by having relatively short tegmina, in which vein Cu_{1a} is strongly angulately bent, and Cu_{1b} is not bent. *C. dorsalis*, by contrast, is without any known close relative, and has not been taken outside St. Vincent, where it is common in high forest. In this species Cu_{1a} is only very weakly angulate and Cu_{1b} is not bent ; the tegmina are relatively longer than in *exquisita*. The natural relationship of all these species is perhaps best expressed by regarding characters of the group (given above) as those of a supergenus *Cenchrea*. Within this are included *Cenchrea*, *Contigucephalus* and *Cenanges*. *Cenchrea* itself may be regarded as comprising two subgenera, of which the typical (*Cenchrea*) includes only *C. dorsalis* while the other includes *exquisita* and its allies, the two groups being distinguished by tegminal characters as given above.

Cenchrea dorsalis Westwood (fig. 10E–I).

Westwood, 1840 : 85.

Anal segment moderately long distally, porrect caudad. Pygofer with laterodorsal angle produced in a straight, narrow, finger-like process. Aedeagus with a complex system of elongate spinose processes, as follows : a pair ventrally at apex directed ventrocephalad below aedeagus ; a pair of very large processes, almost as long as aedeagus, arising near apex and lying along dorsal margin of aedeagus ; a pair of shorter, sinuate lateroapical processes directed dorsocephalad ; a pair of forked blade-like processes lying just mesad of the preceding, and distinctly longer, with a slender curved process attached near base ; a submedian pair of spinose processes dorsally near apex of flagellum ; a second submedian pair of very short curved spinose processes near tip of ventral lip of flagellum, the latter produced at apex in a median decurved spine. Genital styles rather narrow in lateral view, deeply and widely bifid on apical margin ; a stout triangular tooth on inner face at middle, and a semi-membranous flange along dorsal margin directed mesad.

B.W.I. : St. Vincent, Morne Garu, 20.viii.1941, "on *Heliconia bihai*", 14 ♂, 22 ♀ (*R. G. Fennah*).

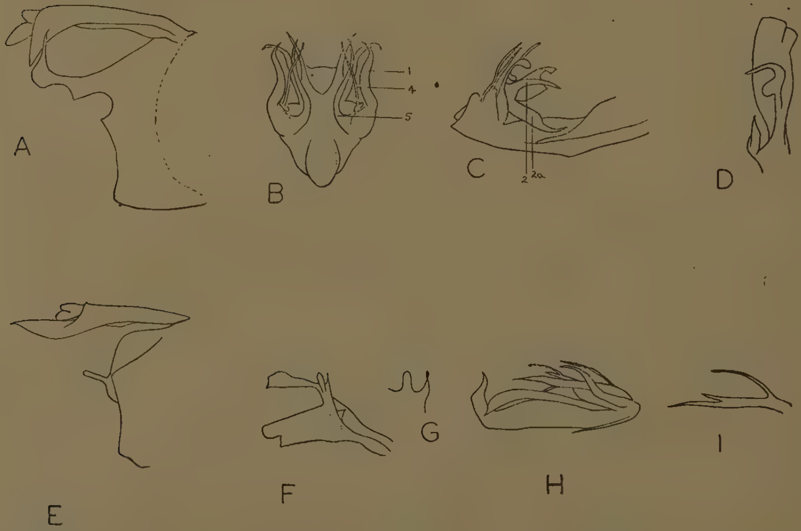

Fig. 10.—*Cenchrea exquisita* Uhl. A, anal segment and pygofer, side view ; B, aedeagus, posterior view ; C, aedeagus, side view ; D, right genital style, dorsal view.
Cenchrea dorsalis Westw. E, anal segment and pygofer, side view ; F, genital style, side view ; G, dorsal processes of genital style, anterior view ; H, aedeagus, side view ; I, compound process of aedeagus.

Cenchrea exquisita Uhler (fig. 10A–D).

Uhler, 1895 : 69.

Anal segment relatively long, abruptly deflexed at apex. Pygofer with laterodorsal angles strongly produced in a narrow process, biconcave on lower margin and abruptly bent dorsad near apex. Aedeagus tubular, with three pairs of spinose processes latero-dorsally near apex, directed dorsad (1, 4, 5 in figure), a pair of stout broad bifid processes laterally (2, 2*a*); flagellum in form of a wide-mouthed trumpet, with a pair of slender processes dorsolaterally at apex, and a pair of broader processes ventrolaterally. Genital styles relatively straight and narrow; a stout spinose process on inner face near base, and a more slender incurved process, produced into a plate near its base, at middle on inner face.

B.W.I.: St. Vincent, Morne Garu, "on *Heliconia bihai*," 20.viii.1941 (*R. G. Fennah*); Grenada, Grand Etang, 7.i.1948, 23 ♂, 29 ♀ (*R. G. Fennah*).

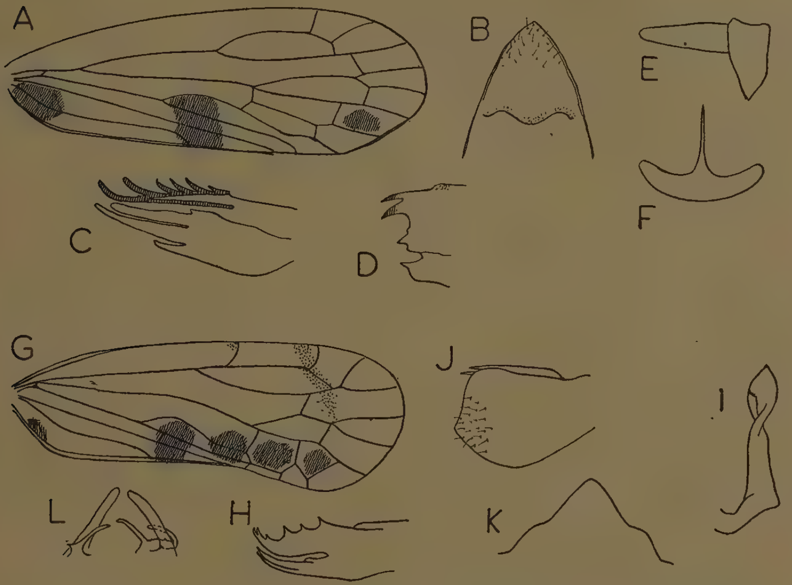

FIG. 11.—*Cenchrea sexguttata* sp. n. A, tegmen; B, apical portion of pregenital sternite, dorsal view; C, first valvula of ovipositor, right side, side view; D, do., ventral view; E, spinose sclerite on wall of vagina at entrance to bursa copulatrix, side view; F, do., dorsal view.

Cenchrea sororia sp. n. G, tegmen; H, first valvula of ovipositor, right side, side view; I, second valvula of ovipositor, right side; J, third valvula of ovipositor, right side, side view; K, posterior margin of pregenital sternite; L, processes in vagina at entrance to bursa copulatrix, dorsal view.

Cenchrea sororia sp. n. (fig. 11G–L).

Female: length, 2·5 mm.; tegmen, 3·1 mm.

Venation of tegmina as figured. Wings with R and M simple, Cu_1 three-branched (2, 1).

Stramineous; mesoscutellum fusco-piceous. Tegmina pallid, translucent, a faint oblique mark at basal edge of stigma; a faint band from costal margin distad of stigma across to M, and between this and apex a narrow, more distinct, line from costal margin to M_{1+2}, brownish-fuscous. An ovate spot in basal fifth of clavus, a short broad band from Cu_1 just distad of fork passing across clavus to commissural margin; three spots in M beyond this band, with the basal pair subequal, fusco-piceous; posterior claval vein and commissural margin of clavus tinged orange.

Anal segment of female small. Pregenital sternite sinuately rectangulately produced caudad. First valvulae of ovipositor with a submembranous bifid lobe ventrally and a sclerotised limb bearing six teeth dorsally; second valvulae terminating in a membranous lobe distinctly twisted in relation to basal portion; third valvulae broad with dorsal margin almost straight, ventral margin convex; a horizontal lobe dorsally. Vagina with a broad sclerotised plate forming ventral surface, and a set of three short teeth on each side. Bursa copulatrix ornamented with sclerotised rings in dense array; an unequally two-pronged process on left and an unequally three-pronged process on right at its entrance.

Holotype, ♀, B.W.I.: Trinidad, 27.i.1929 (*J. G. Myers*) (B.M. 1929–170).

A mutilated female from VENEZUELA: Aragua, Rancho Grande, iii.1949 (Marcuzzi), unquestionably belongs to this species. This species recalls *Cenchrea bipunctata* (Muir) (**comb. nov.**) but differs in the tegminal markings: it is possible that further collecting may show it to be merely a geographical subspecies of *bipunctata*.

Cenchrea sexguttata sp. n. (fig. 11A–F).

Female: length, 2·5 mm.; tegmen, 3·0 mm.

Stramineous, pronotum slightly darker; eyes red. Tegmina translucent, pale yellowish, a spot at base of clavus, another near its apex, and a third in apical cell M_3 fuscous. Insect powdered white.

Anal segment very short. Pregenital sternite subconically produced posteriorly. First valvulae of ovipositor bilobate with upper lobe distally sclerotised and bearing on dorsal margin four subequal teeth with two longer teeth distally, all directed obliquely dorsocaudad; ventral lobe submembranous, deeply cleft distally; second valvulae as in *C. sororia*; third valvulae broad, dorsal margin horizontal, ventral margin convex. Vagina with a pair of dentate processes, each about as long as broad. Bursa copulatrix armed at entrance with a blade-like spine arising from a crescentic sclerite.

Holotype, ♀, BRITISH GUIANA: N.W. District, Mabaruma, 9.v.1929 (*J. G. Myers*) (B.M. 1929–406).

Paratype, 1 ♀, same particulars as holotype.

This species is distinguished by the shape of the genitalia and the coloration of the tegmina.

Cenanges gen. n.

Head with eyes narrower than pronotum; vertex triangular, posteriorly incised, small, deeply hollowed out, rounding evenly into frons, which is medially ecarinate, narrow, gradually widening distally; subantennal processes absent; antennae with basal segment short, cylindrical, second segment round, broader than long; clypeus longer than frons, feebly tricarinate, rostrum distinctly surpassing post-trochanters. Pronotum feebly excavate posteriorly, almost transverse; pronotal disc prominent, with lateral discal carinae more prominent than median carina, and reaching hind margin; lateral marginal carinae prominent, forming a large and deep fovea; mesonotum feebly tricarinate; carinae parallel.

Tegmina with anterior and posterior margins subparallel; apical margin deeply rounded; Sc + R + M stalk forked at base; Sc + R fork about level with union of claval veins; M forked level with apex of clavus and Cu_1 fork basad of this; M with four branches reaching margin, Cu_1 with two; clavus closed. Wings only a little shorter than tegmina; R and M simple to apex, Cu_{1a} furcate near margin, Cu_{1b} simple.

Anal segment of female relatively very small. Lower margin of pregenital sternite in profile straight, continuing line of lower margin of abdomen.

Anal segment of male with lateroapical angles produced. Pygofer with a distinct medioventral process. Genital styles in ventral view triangularly produced mesad at middle and incurved distally.

Type species, *Cenanges spectralis* sp. n.

Cenanges spectralis sp. n. (fig. 12A–H).

Male: length, 4·3 mm.; tegmen, 5·5 mm. *Female:* length, 4·5 mm.; tegmen, 5·9 mm.

Ivory-white; lateral carinae of vertex and frons, a suffusion antero-laterally on mesonotum, and on abdominal tergites and genitalia, fuscous. Tegmina hyaline; middle portion of costal cell, apex of cell R in corium, cell M and Cu in corium, a suffusion over membrane posterior to R at apex brown, faintly fuscous near margin in anal lobe; veins pallid, adjoining areas in corium hyaline. Wings hyaline, veins concolorous, with exception of M and R and Cu_{1a} in part, which are narrowly fuscous. Insect in life powdered pallid.

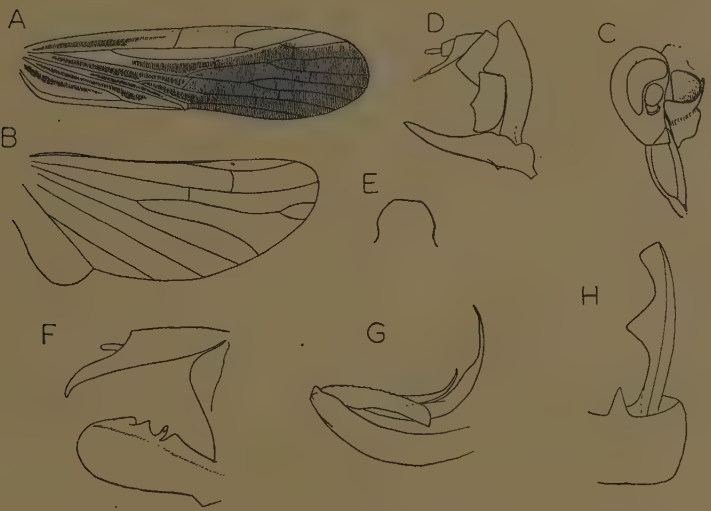

FIG. 12.—*Cenanges spectralis* gen. et sp. n. A, tegmen; B, wing; C, head and pronotum, side view. D, anal segment and genitalia of female, side view; E, posterior margin of pregenital sternite; F, anal segment, posterior margin of pygofer and right genital style, side view; G, aedeagus, right side; H, right genital style, right side of pygofer and medioventral process, ventral view.

Anal segment of male moderately long, distally strongly deflexed; lateroapical angles acute, apical margin deeply incised. Laterodorsal margins of pygofer shallowly rounded, medioventral process acutely triangular. Aedeagus bilaterally symmetrical, a pair of processes arising on each side dorsally at apex, directed cephalad, the outer broad, bladelike, translucent, the inner long, sinuate, serrulate on both sides; flagellum with a pair of broad processes dorsally, distally tapering and curved dorsad, and below these a long membranous tapering process, distally curved dorsad, with a linear sclerite at each margin. Genital styles in profile slightly expanding distally, rounded at apex, with two triangular processes and an outwardly curved spine on dorsal margin.

Pregenital sternite of female broad, slightly narrowed distally, apical margin rounded-transverse.

Holotype, ♂, B.W.I. : Dominica, near Saltoun, 1000 ft. in mountain forest, 12, 19.vi.1939 (*R. G. Fennah*).

Paratype, 1 ♀, same particulars as holotype.

This species runs down in Muir's generic key (1918 : 232) to *Basileocephalus* and in Metcalf's key (1938 : 326) to *Neocenchrea*. It differs from the former in the elevated pronotal disc, in the relatively shorter mesonotum, in the ecarinate and hollowed mesoscutellum, and the shape of the lateral mesonotal carinae : from *Neocenchrea* it differs in the pronotal disc, the much greater development of the upper lateral marginal carinae of the pronotum (upper wall of fovea), in the round, not subangulate shape of the fovea, in the relatively longer rostrum, and longer legs. Species of *Cenchrea* have a moderately short trapezoidal vertex ; in *Cenanges* the vertex is elongate-triangular. In *Cenchrea* the rostrum just attains the post-trochanters, the subcostal cell in the tegmina is short, and vein Cu_{1a} is more or less angulately bent, while Cu_{1b} is almost straight, not angulately bent. In *Cenanges* the rostrum completely surpasses the post-trochanters ; the subcostal cell of the tegmina is long ; vein Cu_{1a} is not at all bent, whereas Cu_{1b} is quite markedly bent. Moreover, in *Cenanges* the tegmina are relatively longer than in *Cenchrea*. In *Cenchrea* the length of the post-tibiae is not or scarcely equal to the greatest width of a tegmen ; in *Cenanges* the corresponding length is 1·5 that of the greatest width of a tegmen ; moreover in *Cenchrea* the male anal segment is elongated, the laterodorsal angles of the pygofer are produced, while no definite medioventral process is developed : in *Cenanges* the male anal segment is not elongate, the laterodorsal angles of the pygofer are not produced, and a medioventral process is present.

Omolicna Fennah.

Fennah, 1945 : 440. Orthotype, *Omolicna proxima* Fennah.

Omolicna proxima Fennah (fig. 13I, K).

Fennah, 1945 : 441.

Tegmina uniformly pale fuscous, veins concolorous, costal cell with a hyaline marginal spot slightly basad of stigma.

Pregenital sternite of female in profile shallowly concave with a transverse callus at base ; lateral sclerite of eighth abdominal segment obovate, posterior border convex throughout.

Aedeagus with three processes on left directed cephalad, subequal in length, the upper two flattened and blade-like ; on right side two equal blade-like processes, from near base of which arise a pair of united flagellar spines, one surpassing the other and dilated distally into an oblique, lanceolate lobe, hollowed beneath, tapering to a point. Genital styles with dorsal process comprising a short spine directed laterad and curved caudad, attached basally to a sinuately-tapering flattened process directed caudad and narrowing to a point.

VENEZUELA : Chivacoa, 24.x.1947, 2 ♂, 1 ♀ (*H. E. Box*).

Omolicna dominicana sp. n. (fig. 13A–F, H).

Male : length, 3·2 mm. ; tegmen, 4·0 mm. *Female :* length, 3·3 mm. ; tegmen, 4·0 mm.

Pallid yellow ; margins of frons and vertex narrowly dark ; metanotum, abdominal tergites and genitalia yellowish-brown. Tegmina sub-hyaline, lightly suffused with yellowish-brown except in costal cell, which is hyaline or, where opaque, greyish-white ; membrane a little darker than corium ; Sc, R, M and base of Cu_1 slightly infuscate, apical veinlets paler than membrane, apical margin in part more or less suffused with pink. Wings faintly tinged fuscous, veins slightly darker. Insect in life powdered white, tinged by ground-colour.

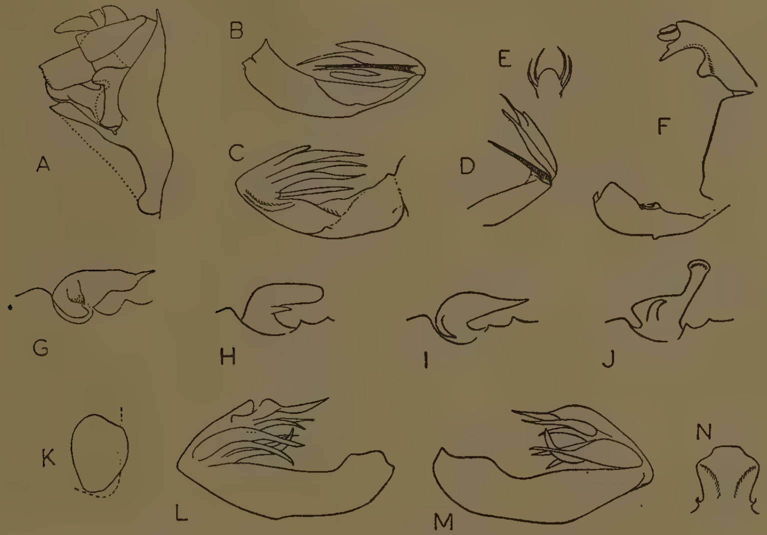

Fig. 13.—*Omolicna dominicana* sp. n. A (solid line throughout), anal segment and genitalia of female, side view ; B, aedeagus, left side ; C, do., right side ; D, do., left side, flagellum elevated ; E, diagram of flagellum in dorsal view, showing arrangement of processes ; F, anal segment, pygofer, and right genital style ; H, process on dorsal margin of genital style.

Omolicna cubana (Myers). G, process on dorsal margin of genital style ; L, M, aedeagus, right and left side ; N, medioventral process.

Omolicna proxima Fenn. I, process on dorsal margin of genital style ; K, lateral sclerite of eighth abdominal segment of female.

Omolicna latens sp. n. J, process on dorsal margin of genital style.

Anal segment of male in profile produced in a deeply rounded lobe at middle of lateral margin ; lateroapical angles acuminate, produced ventrad for a distance equal to length of anal style. Aedeagus tubular, a pair of stout blade-like processes, united at their base, arising on right at base of flagellum, directed cephalad ; on left side, in corresponding position, a single straight rather slender process directed cephalad ; flagellum almost bilaterally symmetrical, with a pair of subequal slightly curved blade-like processes on each side, arising near its base ; apical margin of median dorsal lobe rounded. Genital styles with an incurved spine on ventral margin near base, a short triangular pointed lobe on apical margin directed mesad and dorsad, a compound process in middle of dorsal margin comprising a short spine directed laterad and curved caudad, arising from a stouter process which is rectangulately bent basad of its middle and directed caudad, apically bluntly rounded. Pregenital (seventh) sternite of female in profile markedly concave with a stout transverse callus at base; lateral sclerite of eighth abdominal segment more or less straight along most of posterior margin, but in its dorsal portion produced caudad in a blunt lobe.

Holotype, ♂, B.W.I.: Dominica, Saltoun, "taken in mountain forest," 11.vi.–8.vii.1939 (*R. G. Fennah*).

Paratypes, 20 ♂, 37 ♀, same particulars as holotype.

This species is distinguished by the shape of the male and female genitalia.

Omolicna latens sp. n. (figs. 13J, 24E).

Male: length, 2·8 mm.; tegmen, 3·1 mm. *Female:* length, 3·3 mm.; tegmen, 3·7 mm.

Head, pronotum, legs and membrane of abdomen pallid, mesonotum and sometimes abdominal sclerites yellowish-brown; metanotum and sometimes abdominal sclerites and female genitalia fuscous, eyes dark red. Tegmina hyaline, very lightly infuscate and with a yellow suffusion in cells of corium and clavus; R at apex and a submarginal suffusion fuscous, apical margin tinged with red. Wings sub-hyaline, veins yellow suffused fuscous distally. Insect in life powdered white.

Anal segment of male with lateroapical angles acuminately produced ventrocaudad, ventral lateral margins in profile triangularly produced at basal third. Aedeagus tubular, a long slender spinose process at apex on left side, directed cephalad; mesodorsad of this, on left side of flagellum, a broad blade-like process, slightly deflexed distally and obliquely tapering; a short and slender spine on flagellum just dorsad of base of this process, directed cephalad; on right side a sinuate blade-like tapering process, much longer than all the others, directed cephalad; mesodorsad of this, on base of flagellum, two subequal blade-like processes, distally tapering, decurved then upcurved at apex. Genital styles with mediodorsal process comprising a short spine directed laterad, and curved caudad at apex, arising from the broad base of a club-like process directed caudad and curved laterad distally.

Pregenital sternite of female in profile almost straight, devoid of an obvious transverse callus at base; lateral sclerite of eighth abdominal segment approximately ovate, with posterior margin narrowly and rather deeply excavate at its dorsal third.

Holotype, ♂, B.W.I.: Trinidad, Northern Range, St. John's Valley, "500 ft. in secondary growth," 6.viii.1948 (*R. G. Fennah*).

Paratypes, 2 ♀, same particulars as holotype.

This species is distinguished by tegminal coloration and by the shape of the genitalia in both sexes.

Omolicna cubana (Myers) **comb. nov.** (fig. 13G, L–N).

Phaciocephalus cubanus Myers, 1926: 103.

Dr. W. E. China kindly prepared the figures of the male genitalia reproduced here. They are based upon a paratype from the Myers' Collection.

Phaciocephalus fulvus Van D., *P. uhleri* and *P. brunnea* McAtee belong in this genus.

Oropuna gen. n.

Vertex distinctly broader than long in middle, apically transverse; lateral margins broadly explanate and beset with sensory pits; frons only slightly more than twice as long as broad; disc not depressed, ecarinate, lateral margins not elevated; clypeus slightly shorter than frons, genae devoid of subantennal process; antennae small, second segment scarcely twice as long as broad. Pronotum moderately long, medially carinate, posteriorly shallowly angulately excavate, a deep antennal fovea developed on each side. Tegmina with subcostal cell long. Anal segment of male extremely short. Pygofer with a large subquadrate or trapezoidal medioventral process. Genital styles in ventral view with two processes directed mesocaudad. Aedeagus bilaterally symmetrical.

Hind margin of pregenital sternite of female produced caudad in a semicircular lobe.

Type species, *Phaciocephalus minutianus* Caldwell, 1944 : 102.

This genus is distinguished by the shape of the head, anal segment, medioventral process of pygofer, genital styles and symmetrical aedeagus.

Anchimothon gen. n.

Vertex slightly broader across base than long in middle line, apically concave, lateral margins broadly raised and beset with sensory pits; frons about three times as long as broad, medially ecarinate, margins elevated; clypeus about two-thirds as long as frons, genae without a subantennal process; antennae short, second segment about twice as long as broad. Pronotum moderately broad, posterior margin shallowly concave, medially carinate, a deep antennal fovea developed on each side. Tegmina with subcostal cell long.

Anal segment of male elongate, relatively narrow; anal foramen near apex; apical angles shortly produced ventrad. Pygofer with a deeply rounded medioventral process, longer than broad. Genital styles in ventral view with a lobe directed mesad near base; apical margin curved mesad. Aedeagus bilaterally symmetrical.

Type species, *Phaciocephalus parishi* Muir, 1918 : 418.

This genus is distinguished by the shape of the head, anal segment, and medioventral process of the pygofer, and by the symmetrical aedeagus.

Neocenchrea Metcalf.

Metcalf, 1923 : 193. Orthotype, *Cenchrea heidemanni* Ball, 1902 : 261.

Neocenchrea mero sp. n. (fig. 14A–G).

Male : length, 3·6 mm.; tegmen, 4·8 mm.

Stramineous, in life powdered pallid. Lateral carinae of vertex and frons and a prominent round spot on pronotum behind eyes fuscous. Tegmina milky-hyaline, in life powdered white; a stripe along middle of costal cell; cells between R and M and basal portion of cell M in corium and commissural margin fuscous, the last infuscation extending over Cu_{1b} as a fainter and broader suffusion; apical cells faintly tinged with yellowish brown, apical margin lightly tinged with orange. Veins pale. Wings milky hyaline, veins concolorous.

Anal segment moderately long, latero-apical angles produced and deflexed apically. Pygofer with dorsolateral angles produced in a short broad process, abruptly tapering to a point distally. Aedeagus bilaterally symmetrical, dorsoventrally depressed, shallowly curved dorsad distally, deeply cleft along middle line, each half of aedeagus bearing a long spinose process dorsally lying parallel to upper margin; a stout spine at apex strongly deflexed and slightly curved cephalad distally; a slender spine ventrally, directed ventrad then curved at middle to point caudad; on each side of this spine at its base a minute spine, that on laterad side directed ventrocaudad, that on mesad side directed mesocaudad. Genital styles with a longitudinal dorsolateral ridge on exterior face, a small uncinate process on dorsal margin followed by two rounded-triangular eminences; in ventral view genital styles with mesad borders converging from base almost to meet at middle, then abruptly excavated just distad of middle.

Holotype, ♂, B.W.I.: Trinidad, Aripo Valley, "on bean foliage," 20.ix.1949 (*R. G. Fennah*).

This species is distinguished by coloration and by the shape of the male genitalia.

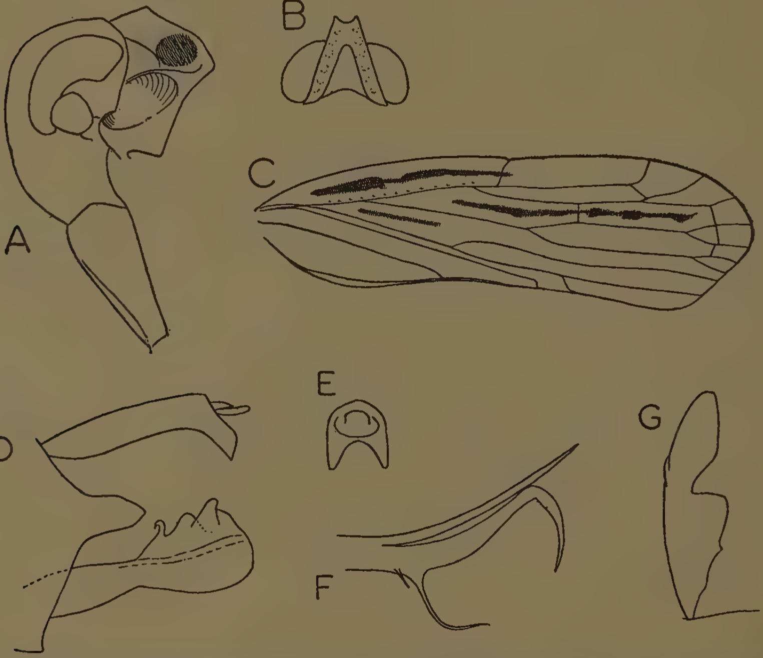

FIG. 14.—*Neocenchrea mero* sp. n. A, head and pronotum, side view; B, head, dorsal view; C, tegmen; D, anal segment, pygofer and left genital style, side view; E, anal segment of male, posterior view; F, aedeagus, left side; G, left genital style, ventral view.

Persis Stål.

Stål, 1862 : 7. Haplotype, *Persis pugnax* Stål, *loc. cit.*

Persis subg. typ.

Head compressed, in profile more or less acutely angulate at apex; vertex elongate, narrow, tapering distally; lateral margins elevated; frons elongate, narrow, with lateral carinae subparallel and raised; eyes excavate posteroventrally; antennae short, subglobose. Pronotum very short, laterally wider, with a low curved ridge behind eyes and lateral margin shallow but definitely laminate, bounding an extremely shallow antennal fovea. Tegmina long, narrow, almost parallel-sided; Sc + R fork slightly basad of middle, M forked about level with apex of clavus, Cu_1 forked about level with Sc + R fork, R and both branches of M forked near apex, Anal segment of male moderately long, relatively narrow, slightly deflexed beyond anal foramen; lateroapical angles acuminately produced; anal foramen situated more than two-thirds from base. Pygofer with a broadly triangular medioventral process. Genital styles with dorsal margin longer than ventral; apical margin, which is shallowly convex or sinuate, consequently very oblique; inner (ventral) margin sinuate, usually with one or more short eminences in basal half; dorsal margin with a broad process at basal third, this process ornamented with about three spines or lobes distally. Aedeagus bilaterally symmetrical. Pregenital sternite of female produced at middle in a deeply rounded or turbinate lobe, this produced area not longer than basal part of sternite.

The species *pugnax* Stål, *fabriciana* Metcalf, *ståli* Muir, *foveatis* Caldwell, and *novacula* (described below) are placed in this sub-genus. They agree closely in general appearance, and share the same colour pattern. *Persis fuscinervis* Muir falls outside the concept defined above, and is referred to a new subgenus.

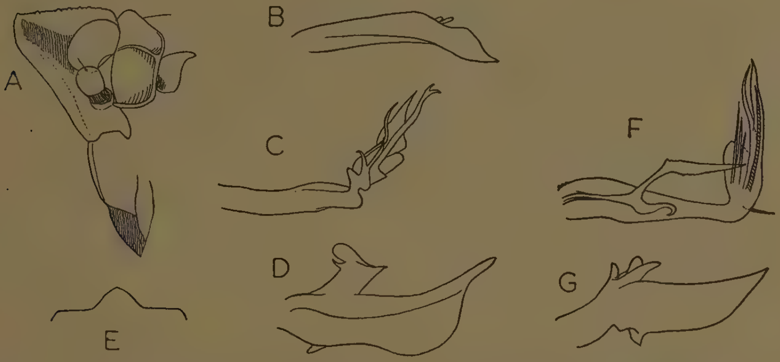

FIG. 15.—*Persis ståli* Muir. A, head, side view; B, anal segment of male, left side; C, aedeagus, left side; D, left genital style; E, medioventral process of pygofer. *Persis novacula* sp. n. F, aedeagus, left side; G, left genital style.

Persis (*Persis*) *ståli* Muir (fig. 15A–E).

Muir, 1918: 417.

Male: length, 4·1 mm.; tegmen, 6·1 mm.

Aedeagus tubular; flagellum with an outer pair of short stout processes at base, each produced distally in an unequal pair of rather short curved spines; mesad of these processes, and arising at about same level, a pair of long slightly sinuate ribbon or blade-like processes, each shortly cleft at apex; a pair of slender, sinuate, moderately long processes; submedially a pair of thin triangular lobes, acuminately produced distally: all these processes extending in the same general direction, cephalad when flagellum is folded. Genital styles with dorsal process subquadrate, large; inner (ventral) margin armed with a blunt tooth near base; apex of style produced, narrow.

BRITISH GUIANA: Kanuku Mts., i.1934, 1 ♂ (*J. G. Myers*).

This species is distinguished by the aedeagal armature and by the shape of the genital styles. Its relation to *P. fabriciana* Metcalf, also apparently from the Guianas, is unknown.

Persis (Persis) novacula sp. n. (fig. 15F, G).

Male : length, 5·4 mm. ; tegmen, 6·3 mm. *Female :* length, 5·6 mm. ; tegmen, 6·5 mm.

Shape and coloration of *P. stâli* Muir.

Anal segment moderately long and narrow with anal foramen at distal third ; apical margin almost semicircularly excavate with apical angle acuminate.

Aedeagus bilaterally symmetrical with an unequally bifurcate process on each side arising at base ; flagellum with a pair of short spatulate lobes anteriorly at base ; behind each of these a close series of three slender spines, equal in thickness but graded in length ; arising slightly above these a longer and slightly thicker spine ; submedially a pair of long lanceolate processes on each side, both shallowly sinuate with the broader pair slightly surpassing the narrower, the latter much narrowed and acuminate distally.

Genital styles moderately long, narrowed and curved slightly dorsad distally, acutely pointed at apex ; basal half of dorsal margin with an eminence bearing three processes, the basal acuminate and curved laterad, the middle dome-like, the distal finger-like.

Holotype, ♂, B.W.I. : Trinidad, Northern Range, Aripo, 500 ft., 17.ix.1949 (*R. G. Fennah*).

Paratypes, 4 ♀, same particulars as holotype.

This species is distinguished by the shape of the aedeagal armature.

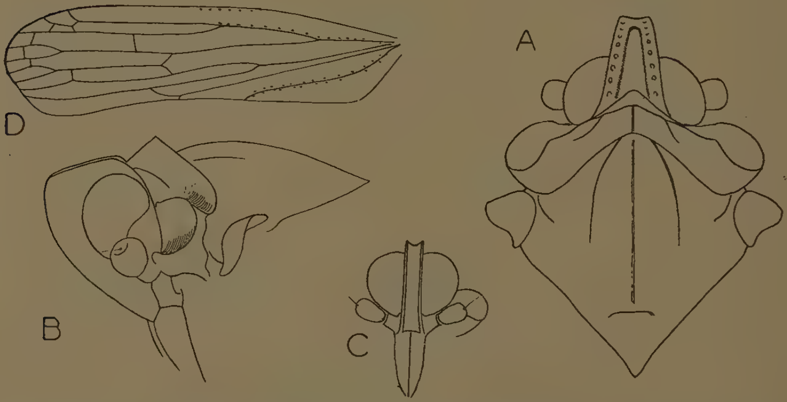

FIG. 16.—*Persis* (*Anapersis spreta*) (Fowl.). A, head and thorax, dorsal view ; B, do., side view ; C, head, anterior view ; D, tegmen.

Persis.

Anapersis subgen. n.

Head with eyes narrower than pronotum ; vertex about 1·5 times as long as broad, with straight sides narrowing anteriorly ; width at apex about half width at base ; anterior margin carinate, transverse ; posterior margin subrectangulately excavate, disc moderately depressed ; lateral margins in profile horizontal, meeting those of frons subangulately ; frons moderately narrow, medially ecarinate ; lateral margins raised, not quite parallel, gradually widening from base to apex ; subantennal process absent ; antennae with first joint short, ringlike, second short, obovate ; clypeus about as long as frons, tricarinate ; rostrum just attaining post-trochanters. Pronotum widely angulately excavate posteriorly ; median carina prominent, elevated ; sublateral areas strongly inclined away from it to lateral margins; lateral marginal carinae forming a fovea, with the dorsal margin foliate, not merely carinate; mesonotum slightly broader than long, feebly tricarinate.

Tegmina long, costal and commissural margins parallel, apical margin anteriorly rounded, then straight and obliquely truncate. Sc + R + M fork at basal fifth, Sc + R forking basad of, and M forked about level with, apex of clavus, Cu_1 forked about level with union of claval veins, Sc and R together with three branches at apical margin, M with four, Cu_1 with two.

Wings ample, only a little shorter than commissural margin of tegmina; R simple to apex, M simple, Cu_1 with two branches.

Anal segment of male relatively long and narrow with anal style near apex. Pygofer with a well-developed medio-ventral process.

Anal segment of female short, broader than long. Pregenital sternite broadly produced and rather deeply rounded on posterior margin, in profile shallowly sinuate.

Type species, *Neocenchrea gregaria* Fennah.

This subgenus is distinguished from typical *Persis* by the prominent pronotal foveae, which are obsolete in *Persis*, and by the narrow form of the medioventral process of the pygofer. The profile of the head is considerably different. The subgenus differs from *Neocenchrea*, to which its type species was originally referred, in shape of head, in the presence of a carina between vertex and frons, in the more strongly developed dorsal margin of the pronotal foveae, in the relatively broader mesonotum, in the shape of the tegmina, in the presence of a medioventral process on the pygofer and in the pattern of the aedeagus and genital styles. *Mysidia ? spreta* Fowler (fig. 16A–D) is here transferred to this subgenus, to which also *Neocenchrea pallescens* Metcalf appears to belong.

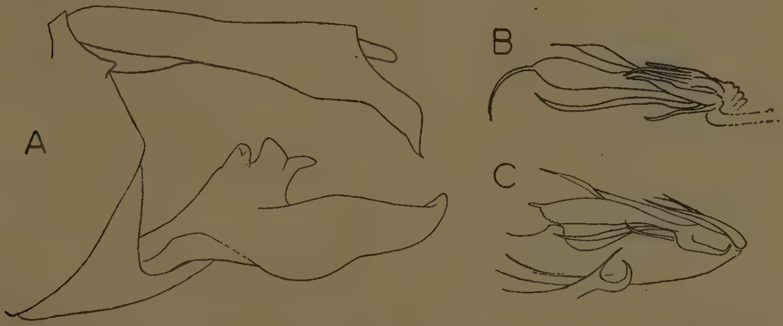

FIG. 17.—*Persis* (*Anapersis*) *gregaria* (Fenn.). A, anal segment, pygofer and left genital style, side view; B, aedeagal flagellum and appendages, reflected caudad, right side; C, aedeagus, apical portion, left side.

Persis (*Anapersis*) *gregaria* (Fennah) (fig. 17A–C).

Persis lineata Uhler, 1895: 69.
Neocenchrea gregaria Fennah, 1945b: 443.

B.W.I.: St. Vincent, Petit Bordel, 19.viii.1941, 3 ♀; Grenada, Grand Etang, 28.x.1943, 2 ♂, 3 ♀; Grenada, St. George's, Mt. Wheldale, 16.viii.1947, 1 ♂, 2 ♀; St. Lucia, Quilesse, 22–24.ii.1941, 1 ♂ 1 ♀ (all *R. G. Fennah*).

The figure is of a specimen from Grenada.

Persis

Eritalaena subgen. n.

Vertex with lateral margins in profile horizontal, little produced beyond level of eyes, rounding into base of frons ; frons moderately narrow, medially ecarinate, lateral margins elevated, subparallel ; no subantennal process on genae ; antennae with first segment short, ring-like, second short subovoid ; clypeus about as long as frons. Pronotum with marginal carinae obsolete, no antennal fovea developed.

Tegmina long, costal and commissural margins parallel, apical margin rounded. Sc + R + M fork at basal fifth, Sc + R forking basad of, and M forked about level with, apex of clavus ; Cu_1 forked almost level with union of claval veins, Sc and R together with three branches at margin, M with four and Cu_1 with two.

Anal segment of male relatively long and narrow with anal style near apex. Pygofer with a short triangular medioventral process.

Anal segment of female short, broader than long. Pregenital sternite produced on hind margin in a large deeply rounded lobe which is longer than basal part of sternite.

Type species, *Persis fuscinervis* Muir, 1918 : 417.

This subgenus is distinguished from the typical subgenus and from *Anapersis* by the shape of the head in profile, by the absence of distinct lateral carinae on the pronotum, by the shape of the medioventral process of the pygofer and of the posterior lobe of the pregenital sternite.

Goneokarella gen. n.

Frons longer than broad (1·6 : 1), transverse at base ; lateral margins slightly diverging to below level of antennae, thence incurved to suture, which is subequal in width to base ; vertex slightly more than twice as broad across base as long in middle, laterally carinate, devoid of median carina ; frons and clypeus medially and laterally carinate throughout ; lateral ocelli distinct ; antennae with first joint very short, second segment ovoid, 1·5 times as long as broad. Pronotum short, disc tricarinate, a pair of carinae at each side between eyes and tegulae ; lateral foveae absent, lower margin of lateral lobes rounded ; mesonotum tricarinate ; lateral carinae arcuately divergent basad, median carina not complete basally. Post-tibiae with a small spine at base and at middle.

Tegmina 3·6 times as long as broad ; Sc + R united to base of stigma, M four-branched, Cu_{1a} and Cu_{1b} simple ; wings with R and M simple.

Type species, *Goneokarella maculivenis* sp. n.

Goneokarella maculivenis sp. n. (fig. 18A–K).

Female : length, 3·5 mm. ; tegmen, 5·0 mm.

Fusco-piceous ; basal angles of clypeus, carinae of vertex, pronotum and mesonotum, margin of tegulae, a spot on mesonotum behind tegulae, margin of scutellum, margin of pleurites, femora at base and apex, tibiae in middle and at apex stramineous. Tegmina with corium mostly ivory-hyaline, veins overlain fuscous, Sc with about four pallid spots before transverse line ; M with three spots, Cu_1 with one ; membrane fuscous, transverse and most of apical veins, a spot across distal half of apical cells of M and Cu_{1a} and an elongate spot beyond apex of clavus ivory-hyaline ; clavus fuscous, pale on basal fifth and penultimate fifth. Wings slightly smoky.

Anal segment short. Ovipositor with first valvulae bilobate, the lower lobe upcurved, distally bifid with both limbs acuminate ; upper lobe with five stout teeth ; second valvulae as figured, third valvulae broadly quadrate with distal margin slightly oblique, a horizontal lobe attached dorsally on inner face. Pregenital sternite produced at middle of hind margin in a deep rounded lobe. Vagina ornamented with a plate bearing four blade-like processes equidistantly separated; bursa copulatrix ornamented with a small plate bearing a single stout spine, decurved distally.

Holotype, ♀, ARGENTINA: Territory of Rio Negro, 18–25.xi.1926 (*F.* and *M. Edwards*) (B.M. 1927–63).

Goneokarella runs to *Vekunta* in Muir's key, but differs in shape of frons and vertex, in pronotal structure and in tegminal venation. This species is closely similar to a plectoderine achilid such as *Amblycratus*. The genus is isolated, but is perhaps nearest to *Phrygia*: the head in slight degree recalls that of *Cedusa* (though a subantennal process is lacking); the tricarinate pronotal disc can be compared only with the condition found in the *Cenchrea* group of species, in *Phrygia*, or—at great remove—in *Vinata*. The tegminal venation, while relatively unspecialised, is unusual in that a row of subequal subapical cells is formed. This development may be interpreted as an intermediate stage between the usual condition (as in *Vekunta*) and that of *Vinata*.

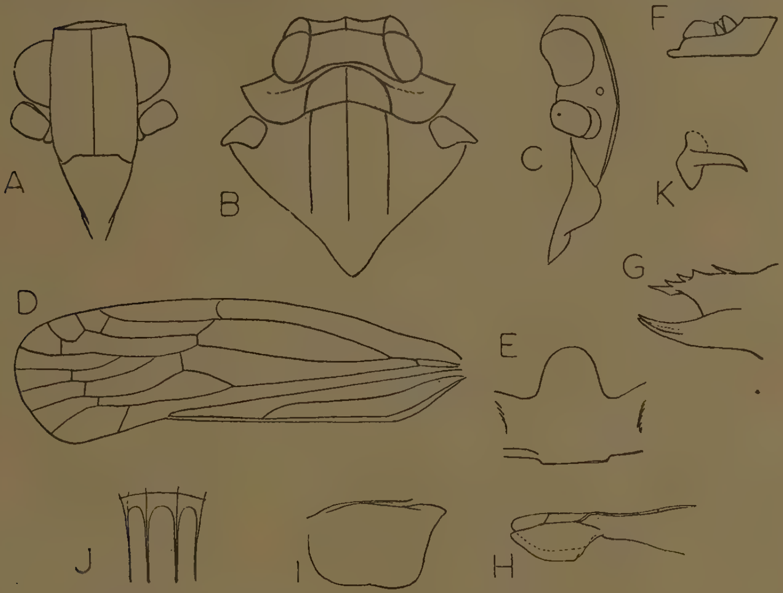

FIG. 18.—*Goneokarella maculivenis* gen. et sp. n. A, head, anterior view; B, head and thorax, dorsal view; C, head, side view; D, tegmen; E, posterior margin of pregenital sternite; F, anal segment of female, right side; G, right first valvula of ovipositor, side view; H, second valvulae of ovipositor, slightly dorsolaterally viewed; I, left third valvula of ovipositor; J, sclerite at entrance to bursa copulatrix; K, sclerite on bursa copulatrix.

Cedusa Fowler.

Fowler, 1904: 112. Logotype, *Cedusa funesta* Fowler.

Cedusa funesta Fowler (fig. 19A–C).

Fowler, 1904 : 112, pl. 11, figs. 28, 28*a–b*.

The figures have been prepared by Dr. China from the type.

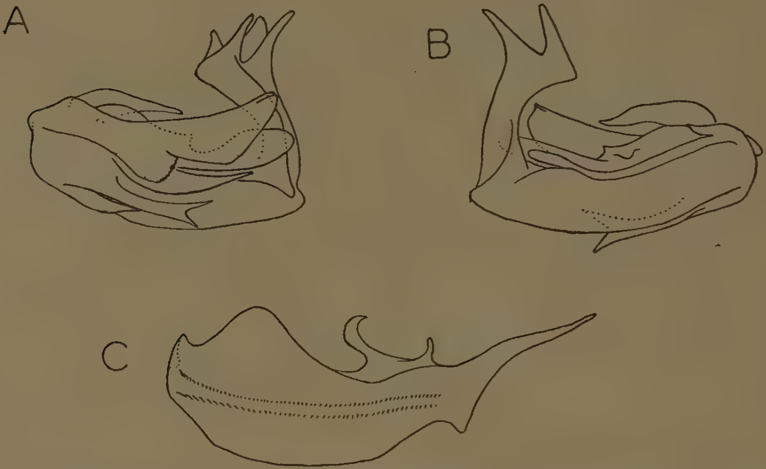

Fig. 19.—*Cedusa funesta* Fowl. A, aedeagus, right side ; B, aedeagus, left side ; C, right genital style, side view.

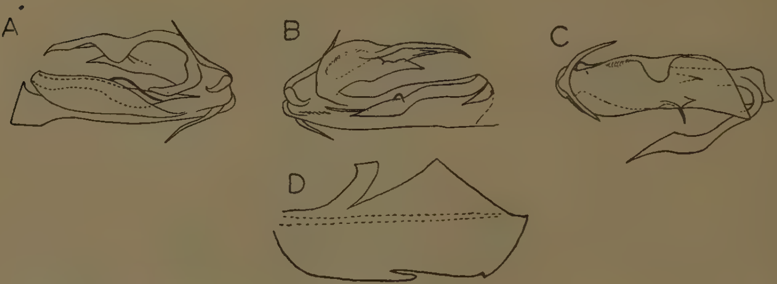

Fig. 20.—*Cedusa albolineata* sp. n. A, aedeagus, left side ; B, do., right side ; C, do., dorsal view ; D, left genital style, side view.

Cedusa albolineata sp. n. (fig. 20A–D).

Male : length, 2·4 mm. ; tegmen, 3·6 mm.

Fuscous to fuliginous ; frons and clypeus in middle line and at margins, subantennal processes in part, antennae, lateral fields of pronotum narrowly at margins, and legs testaceous-stramineous. Tegmina sooty, membrane slightly paler ; node and a portion of each cross-vein on nodal line to apex of clavus narrowly white ; veins concolorous. Wings hyaline, powdered white, with fuscous veins.

Aedeagus tubular; a small slender spine ventrally near apex directed cephalad; an asymmetrical pair of stout shallowly-curved spines arising from a common stem at apex; two spines arising at base of flagellum, that on right moderately long, very slender, sinuate, directed cephalad, that on left long and broad, sinuate, directed cephalad as far as base of aedeagus, then curved sharply to right to point caudad, slightly constricted in middle portions of its length, obliquely truncate distally; flagellum with left margin widely excavated with a lobe at each end of excavation, abruptly and convexly tapering distally to a short deflexed spine at apex, a short, broad submembranous process near middle of right margin of flagellum, and a similar process, subfoliate and horizontal, underlying apical portion of flagellum in its apical third. Genital styles with ventral (inner) margin produced mesad near middle and at apex, dorsal margin produced at its basal third in a short, vertical flattened process, distally truncate; distad of this process dorsal margin shallowly triangularly produced.

Holotype, ♂, VENEZUELA: Chivacoa, 24.x.1947, "taken on sugar-cane" (*H. E. Box*).

This species is distinguished by the aedeagal armature and the shape of the genital styles.

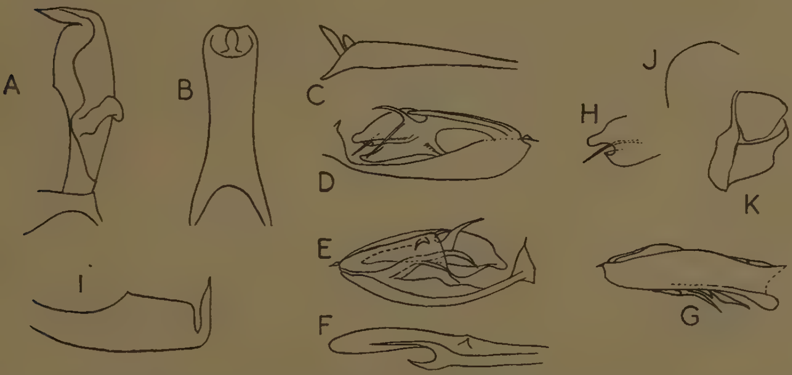

FIG. 21.—*Cedusa inflata dominicana* subsp. n. A, left genital style, dorsal view; B, anal segment, dorsal view; C, do., side view; D, aedeagus, left side; E, do., right side; F, process of left side of aedeagus, semi-diagrammatic; G, aedeagus, ventral view; H, apex of flagellum, left side; I, right genital style, ventral view; J, profile of vertex and basal part of frons; K, sclerites of seventh and eighth abdominal segments of female, left side.

Cedusa inflata (Ball).

Lamenia inflata Ball, 1902: 262.

Cedusa inflata dominicana subsp. n. (fig. 21A–K).

Male: length, 3·0 mm.; tegmen, 3·8 mm. *Female:* length, 3·1 mm.; tegmen, 3·9 mm.

Fuscous; median disc of frons and clypeus testaceous; sides of head and coxae slightly paler; rostrum and legs stramineous to creamy-white; external female genitalia dark fuscous. Tegmina uniformly fuscous; veins concolorous, with exception of transverse veins in membrane, which are hyaline. Wings infumed, veins darker, a line along anal fold hyaline. Insect in life powdered with pale wax, so as to appear smoky-blue.

Aedeagus tubular; flagellum with a minute curved spine at base directed posteriorly, arising on left side; a long sinuate spine on right arising near base, directed cephalad above aedeagus; below this a broad sclerotised plate, shallowly trough-like along middle, tapering to a point distally, left margin or submargin strongly sinuately sclerotised; below this again a stout sclerotised process on left side directed cephalad, forking distally into a pair of short curved spines, at the same level expanded mesad in a broad thin plate, with a small triangular tooth near the point of origin of the two spines. Genital styles as in *C. funesta*, the longer limb of the basal process on the dorsal margin approximately mushroom-shape or clavate in side view.

Holotype, ♂, B.W.I.: Dominica, Saltoun, "1000 ft. in mountain forest," 11–30.vi.1939 (***R. G. Fennah***).

Paratypes, 6 ♀, same particulars as holotype. This is here recognised as a subspecies of *C. inflata* Ball, distinguished from the Haitian type by differences in the shape of the inner (ventral) margin of the genital styles. It otherwise agrees with the published data on *inflata*, but the relationship between Haitian and Dominican material cannot be finally settled without comparison of aedeagal structures.

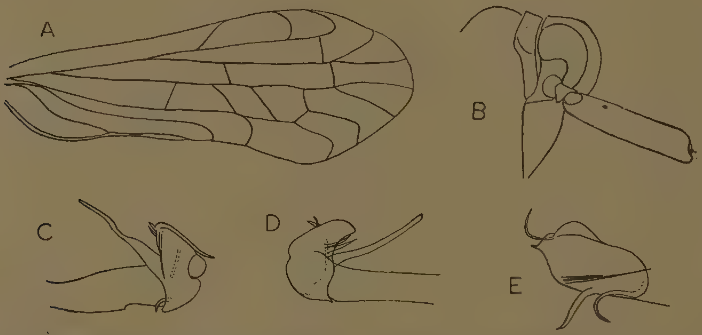

Fig. 22.—*Patara guttata* Westw. A, tegmen; B, head and pronotum, left side; C, aedeagus, right side; D, aedeagus, left side.
Patara fumipennis sp. n. E, apical portion of aedeagus, anterior view.

Patara Westwood.

Patara Westwood, 1841 : 13. Logotype, *Patara guttata* Westwood.

Patara guttata Westwood (fig. 22A–D).

Westwood, 1840 : 85.

Aedeagus asymmetrical with a short spine arising ventrally near apex, curved cephalad and to left; near anterior margin of flagellum a slender spine directed ventrad, lying close above the thickened subvertical ridge on left side; arising submedially below this from a transverse strut a long sinuate process obliquely truncate at apex, directed cephalad; apex of flagellum narrowly triangular and produced in a short acuminate process directed caudad; on right side of aedeagus near apex a very short two-pronged process directed cephalad, and arising slightly posteriorly to its base a moderately long spine directed obliquely.

B.W.I.: St. Vincent, Morne Garu, 20.viii.1941, 44 ♂, 67 ♀ (*R. G. Fennah*).

Of these approximately a quarter, including both sexes, have the tegmina, when freed of wax, mostly infuscate, another quarter is pale, and marked almost exactly as pale *Patara* from other islands, while the remainder are intermediate in varying degrees. *P. albida* Westw. (*ibid.*) as described and figured agrees with the pale form of *P. guttata*. There are no genitalic differences between the colour-forms.

Patara cyanea sp. n. (fig. 23A, B).

Male: length, 2·1 mm.; tegmen, 3·4 mm. *Female:* length, 2·8 mm.; tegmen, 4·0 mm.

Fuscous; clypeus, rostrum and legs ivory-white. Tegmina fuscous; apical margin and apical veins, at least distally, pallid, hyaline; veins otherwise concolorous. Wings fuscous, paler basally, veins concolorous.

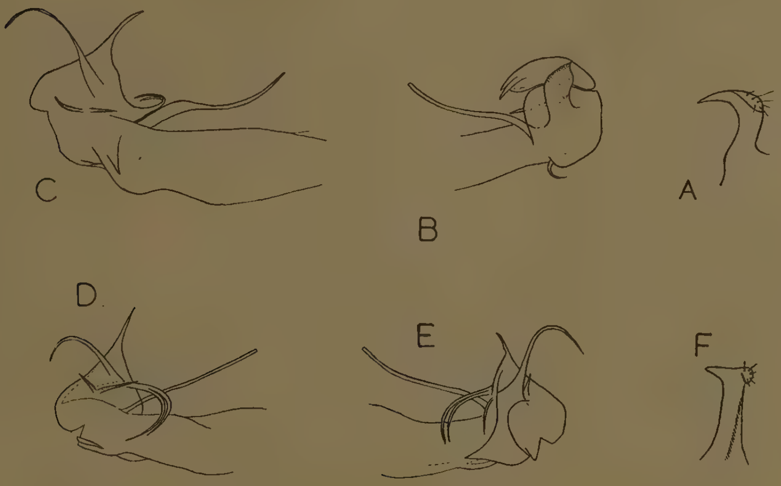

FIG. 23.—*Patara cyanea* sp. n. A, process on dorsal margin of genital style; B, aedeagus, left side.

Patara mimula sp. n. C, aedeagus, right side (Montserrat, B.W.I.); D, do. (Dominica, B.W.I.); E, do., left side (Dominica, B.W.I.); F, process on dorsal margin of genital style (Dominica, B.W.I.).

Anal segment, pygofer and genital styles as in *P. guttata*. Aedeagus with a short spinose process ventrally on right near apex curved to left; a rather long, slender process on right side distally, directed ventrolaterad; a short bifurcate process on right anterior margin of flagellum, directed cephalad: a long sinuate process medially arising from flagellum, directed cephalad; on left side of flagellum a broad flattened process directed dorsad, shortly produced in a point directed dorsocaudad.

Holotype, ♂, B.W.I.: Dominica, near Saltoun, "1000 ft. in mountain forest," vi.1940 (*R. G. Fennah*).

Paratypes, 1 ♂, 1 ♀, same particulars as holotype.

This species is distinguished from *P. guttata*, to which it is very closely allied, by the genital armature, particularly in the absence of a spine on the flagellum directed ventrocaudad.

Patara mimula sp. n. (figs. 23C–F, 24D).

Male : length, 1·6 mm. ; tegmen, 3·1 mm. *Female :* length, 2·7 mm. ; tegmen, 3·4 mm.

Second antennal segment of male longer than broad (3·4 : 1).

Ivory-white ; a spot before eyes, a suffusion dorsally at base and ventrally at apex on antennae, pronotum and mesonotum laterally, and abdominal sclerites brown to fuscous. Tegmina marked exactly as in *P. inermis*, but with all markings on corium darker and larger and spot at apex of costal cell expanded to overlie Sc + R fork. Wings pearly-hyaline. Insect in life powdered white.

Anal segment of male short, latero-apical angles not produced. Pygofer with latero-dorsal angles not produced, medioventral process absent. Genital styles broad, upcurved distally ; apical margin convex, process on dorsal margin as figured. Aedeagus asymmetrical, a short spine arising at apex on right directed cephalad beneath aedeagus ; a pair of spines on right, one, the shorter, directed dorsocaudad, the other directed dorsocephalad ; a long slender process arising dorsally near base of flagellum directed dorsocephalad ; a two-pronged process arising anteriorly on flagellum near right side curved to left, then ventrad ; a median slender spinose process arising dorsally near apex, directed dorsad, then curving caudad and finally ventrad ; flagellum in form of a shallowly curved triangular lobe, partly surrounding base of preceding process, and itself tapering dorsally into a delicate oblique spine.

Holotype, ♂, B.W.I. : Dominica, near Morne Gay, " 1600 ft. in mountain forest," 8.vii.1939 (*R. G. Fennah*).

Paratypes, 4 ♀, same particulars as holotype ; 4 ♂, 2 ♀, DOMINICA : Saltoun, " 1000 ft. in mountain forest," 11–30.vi.1939 (*R. G. Fennah*).

This species is distinguished by the aedeagal armature.

The following additional specimens are also to be assigned here : ST. KITTS : Ottley's Level, " in forest," 26.i.1942, 1 ♂, 1 ♀; ST. KITTS : Brimstone Hill, 28.i.1942, 3 ♂, 1 ♀; NEVIS : Nevis Mountain, " forest," 18.i.1942, 2 ♂; MONTSERRAT : Chance's Mountain, 18.i.1939, 5 ♂, 21 ♀ (all *R. G. Fennah*).

A short series from St. Lucia from the tunnels made by passalid larvae in the rotting trunks of felled trees is assigned to this species, but is recognised as a distinct geographical subspecies, **Patara mimula unicornis** subsp. n., distinguished by having only a single spine on the right side of the aedeagus distally where, in *P. mimula mimula*, there are two spines diverging from a common base.

Holotype, ♂, B.W.I. : ST. LUCIA : Quilesse, " 1000 ft., in the tunnels of Passalid larvae in felled trees," 21.iii.1939 (*R. G. Fennah*).

Paratypes, 2 ♂, 9 ♀, and 34 nymphs, same particulars as holotype.

Patara fumipennis sp. n. (fig. 22E).

Male : length, 1·9 mm. ; tegmen, 3·0 mm. *Female :* length, 2·3 mm. ; tegmen, 3·2 mm.

Fuscous ; clypeus, rostrum, antennae at apex, sides of head immediately before eyes, ivory white. Tegmina fuscous, apical margin and all apical veinlets near margin hyaline-pallid, veins otherwise concolorous. Wings infumed, apical margin narrowly pallid.

Anal segment of male short, latero-apical angles shortly produced. Pygofer with latero-dorsal angles not produced, medioventral process absent. Genital styles as in *P. guttata.* Aedeagus asymmetrical, a two-pronged process, with the dorsal limb shorter, on right side porrect cephalad; flagellum with a slender spinose process directed dorsally, curved through a right angle and directed laterad to left at apex; a long bifurcate process arising near right lateral margin of flagellum directed cephalad and to left; apex of flagellum dorsally produced in a subspinose triangular eminence; an elongate sinuate process medially directed cephalad, and directly below it, arising from the lower margin of the flagellum, a deeply sinuate process curved dorsad, then cephalad to lie parallel with the medial process above.

Holotype, ♂, B.W.I.: St. Lucia, near Castries, "800 ft. in secondary growth," 3.ii.1940 (*R. G. Fennah*).

Paratypes, 3 ♀, same particulars as holotype.

This species is distinguished by aedeagal armature; the usual short spine arising ventrally on the right side and directed to the left below the aedeagus is replaced, as it were, by the long deeply-sinuate spine developed from the lower flagellar margin.

Patara gausapata sp. n. (fig. 26A–G).

Female: length, 2·3 m.m.; tegmen, 3·2 mm.

Ivory-white; margins of frons, a spot on genae before eyes, margins of second antennal joint and abdominal sclerites infuscate; a linear stripe parallel with hind margin of eyes, and median carina of mesonotum at middle; tibiae at apical margin and tarsi at base almost piceous. Tegmina brown with three broad, transverse bands in costal cell, and borders of apical veins hyaline; transverse veins of corium fuscous. Wings hyaline, powdered white.

Antennae ovate, distinctly compressed, eyes not reaching frontoclypeal suture. Rostrum just reaching to base of hind femora. Vertex more shortly triangular than in type species; frons distinctly more compressed, projecting before eyes for half length of an eye. Frontal carinae contiguous to apex. Pronotum medially carinate, lateral marginal carinae feeble, no fovea present. Mesonotum in lateral view strongly convex, ascending from base (excluding mesoscutellum) and apex to the middle, which is distinctly carinate in middle line. Post-tibiae with six stout spines at apex, basal metatarsal joint with six spines on apical margin, second metatarsal joint with five spines on apical margin. Tegmina about 2·3 times as long as greatest width, costal, apical and commissural margins markedly sinuate.

Anal segment of female short. Pregenital sternite broadly triangulately produced on posterior margin. Lateral sclerites of eighth segment trapezoidal, acute dorsally, as in *P. guttata.*

Holotype, ♀, B.W.I.: St. Vincent, near Three Rivers Settlement, "1000 ft. in mountain forest," 5.ix.1941 (*R. G. Fennah*).

This species is strongly distinguished by the shape of the antennae and tegmina and by markings. It stands so far apart from the other species that it may eventually have to be recognised as subgenerically different.

Patara inermis sp. n. (fig. 24A–C).

Male: length, 1·9 mm.; tegmen, 3·0 mm. *Female:* length, 1·8 mm.; tegmen, 3·0 mm.

Second antennal joint four times as long as broad.

Ivory-white, a suffusion on margins of frons and sometimes on genae before eyes; second antennal joint, mesopleurites at base of mesocoxae, and abdominal sclerites lightly infuscate. Tegmina pearly hyaline, in life powdered white; two small spots in costal cell, one at base of M; a suffusion along sides of R, M and Cu in corium, expanding in membrane, except in M, to cover most of apical cells fuscous; veins pallid except transverse veins between R and M, one apical veinlet of R and two apical veinlets of M in part, which are infuscate. Wings pearly-hyaline, powdered white.

Anal segment of male short, latero-apical angles shortly but acutely produced. Pygofer with laterodorsal angles not produced, medioventral process absent. Genital styles broad, upcurved distally, apical margin strongly convex, a rather long process on dorsal margin. Aedeagus asymmetrical, a spine arising at apex directed cephalad beneath aedeagus; a pair of spines on right, one more than twice length of the other, porrect cephalad; flagellum comprising a broad flattened process on left, directed cephalad, curved upward and tapering to a point; a straight slender spine at apex directed dorso-cephalad, a pair of short subsidiary processes, one spinose, the other triangular, on anterior face, the spinose process in direct line above the broad flattened process.

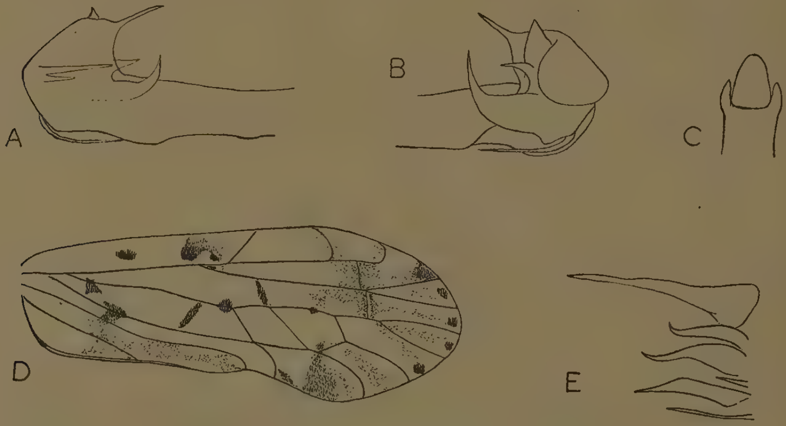

FIG. 24.—*Patara inermis* sp. n. A, aedeagus, right side; B, do., left side; C, anal segment, dorsal view.
Patara mimula sp. n. D, tegmen.
Omolicna latens sp. n. E, processes of aedeagus, separated, semi-diagrammatic.

Holotype, ♂, B.W.I.: St. Lucia, Castries, Morne Fortunée, 1.xii.1938 (*R. G. Fennah*).

Paratypes, 16 ♂, 24 ♀, same particulars as holotype.

This species is distinguished by the shape of the aedeagus.

Patara pakaraima sp. n. (fig. 25A–G).

Male: length, 2·3 mm.; tegmen, 3·5 mm.

Pallid, powdered greyish white, a suffusion across frons and on each side of head before eyes, a small spot on each side of suture below antennae, second segment of antennae, a slight suffusion on mesonotum and sublaterally on tergites of abdomen, fuscous. Tegmina pallid, two quadrate spots in costal cell fuscous; a round spot distad of Sc + R and M fork, a narrow oblique band from Cu across middle of clavus; a broad fascia from R near middle to sutural angle giving off two short oblique stripes on basal side ; a suffusion over apical cells of Sc, R and M_1, reaching margin between apical veins, pale brown.

Anal segment short, broader than long, latero-apical angles produced slightly in short rounded lobes. Pygofer short, posterior lateral margin convex, ventral margin transverse. Aedeagus tubular, hollowed on ventral surface near base, slightly curved upward distally,

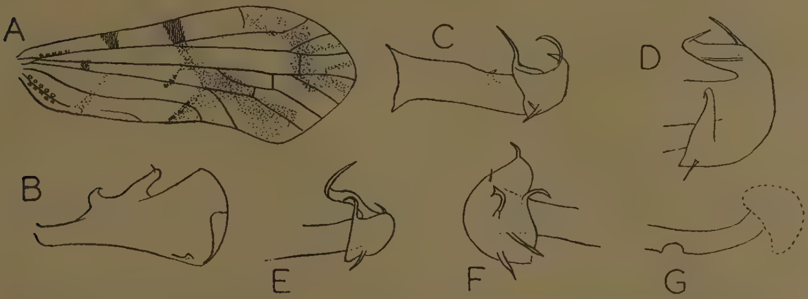

FIG. 25.—*Patara pakaraima* sp. n. A, tegmen ; B, right genital style, inner aspect ; C, aedeagus, ventral view ; D, apex of aedeagus, ventral view ; E, apex of aedeagus, left side, lateroventral view ; F, apex of aedeagus, dorsal view ; G, diagram of aedeagus in profile, showing ventral concavity near base.

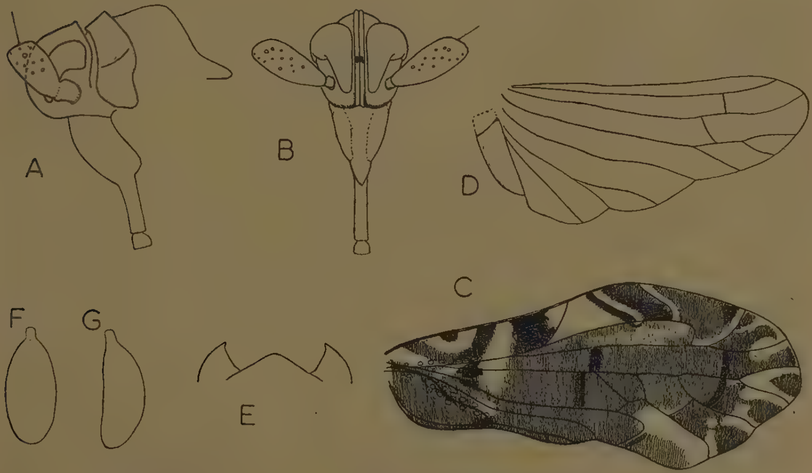

FIG. 26.—*Patara gausapata* sp. n. A, head and pronotum, side view ; B, head, anterior view ; C, tegmen (broken line indicates condition in *P. guttata*) ; D, wing ; E, posterior margin of pregenital sternite ; F, G, egg, anterior and side view.

expanding at apex into a hemispherical cap ornamented as follows : on right, a short spine latero-dorsally, with a blade-like, distally furcate process curved laterad arising below it, a narrow spine directed obliquely ventro-cephalad arising below the preceding, followed in turn by a short spine directed rather more ventrad ; on left, dorsally a large spine bent through 90° to point laterad to left; arising from lower part of cap a spine directed dorsad and recurved at tip, at apex of cap a small spine directed dorsad. Genital styles spatulate, an elongate lobe on dorsal margin with a short curved tooth at its basal end and a furcate process distally; apical margin incurved, a small lobe on inner face near ventro-apical angle.

Holotype, ♂, BRITISH GUIANA: Pakaraima Mountains, near head of R. Mazaruni, 1932 (*J. G. Myers*) (H.3068, B.M. 1933–400).

This species resembles *P. vittatipennis* Fennah in tegminal markings, but differs from this, as from all other species, in shape of genitalia.

TRIBE OTIOCERINI.

In this tribe the head, antennae and tegmina show remarkable variation, though within comparatively narrow limits: the head, however bizarre, is narrow even at its broadest development; the tegmina relatively long; the apical cells, at least in M, always short. The great plasticity of the head, even between sexes in *Swezeyia*, makes its characters undependable for rigorous generic separation. It is likely that when sufficient material has been examined it will be found that the relationship of several concepts at present generic will be more accurately expressed by a subgeneric classification. *Kamendaka* is an acceptable basis of reference in this respect. With series of varied *Anotia* before him the writer found intermediate stages in characters which serve to distinguish *Anotia bonnetii* Kby. from *Amalopota uhleri* Van Duzee, and accordingly cannot at present recognise *Amalopota* as a separate genus, or even as a subgenus.

Labicerus is omitted from the key. Antennal characters associate it with the *Otiocerus* group or with *Iquitosa*, while the size would seem to place it with the former.

Key to Genera of Otiocerini.

(1) (2) Media not arising from radius or arising basad of Sc + R fork (3)
(2) (1) Media arising from radius distad of Sc + R + M fork . . . (71)
(3) (4) First (basal) median sector arising before apical third of tegmen (5)
(4) (3) Median sectors confined to apical third of tegmen . . . . (59)
(5) (6) First segment of antennae short, as broad as long or broader . (7)
(6) (5) First segment of antennae more than twice as long as broad . (51)
(7) (8) Sc + R fork at or basad of middle of tegmen, subcostal cell elongate . . . . (9)
(8) (7) Sc + R fork distad of middle, subcostal cell short . . . . (47)
(9) (10) Subantennal process absent or very small; lateral pronotal carinae absent or very small . . . . (11)
(10) (9) Subantennal process well developed . . . . (35)
(11) (12) Head in profile apically forming a curve, or subconical; frons not wider at base than at apex . . . . (13)
(12) (11) Head in profile angulate at apex, or frons wider at base than at middle . . . . (27)
(13) (14) Vertex little produced beyond eyes; anterior margin in profile subparallel to anterior margin of eye . . . . (15)
(14) (13) Vertex considerably produced beyond eyes . . . . (17)
(15) (16) Frontal carinae rarely contiguous at base **Pyrrhoneura** subgen. **Pyrrhoneura** Kirk.

(16) (15) Frontal carinae contiguous at base **Pyrrhoneura** subgen. **Tempora** Mats.

(17) (18) Antennae not reaching as far as apex of head . . . . . . (19)

(18) (17) Antennae reaching to apex of head ; if not, then base of costal margin of tegmina triangularly produced . . . . (21)

(19) (20) Vertex not two-thirds as long as mesonotum ; tegmina broadest two-thirds from base . . . . **Cobacella***

(20) (19) Vertex at least as long as mesonotum ; tegmina broadest three-quarters from base . . . . **Swezeyia** Kirk.

(21) (22) Vertex and frons in profile deeply and evenly rounded ; apical cells in tegmina not twice as long as broad . . **Kuranda** Dist.[2]

(22) (21) Vertex and frons in profile subconical or narrowly rounded ; most apical cells in tegmina more than twice as long as broad (23)

(23) (24) Costal margin near base produced in a triangular reflected lobe (25)

(24) (23) Costal margin not produced . . . . **Anotia** Kby.

(25) (26) Mesonotum bituberculate ; antennae with appendage **Iquitosa** Fenn.

(26) (25) Mesonotum smooth, antennae simple . . . . . . **Sayiana** Ball

(27) (28) Frons basally at least as wide as at apex . . . **Swezeyia** Kirk.

(28) (27) Frons narrower at base than at apex . . . . (29)

(29) (30) Vertex in profile sinuate . . . . **Kampulokara** Muir

(30) (29) Vertex not as above . . . . (31)

(31) (32) In profile vertex meeting frons rectangulately ; frons strongly convex, especially distally **Kamendaka** subgen. **Eosaccharissa** Kirk.

(32) (31) Vertex and frons in profile meeting at an acute angle ; frons in profile not deeply convex . . . . (33)

(33) (34) Vertex and frons in profile meeting at angle of about 45° **Kamendaka** subgen. **Nicertoides** Mats.

(34) (33) Vertex and frons in profile meeting at angle between 45° and 80° . . . . **Kamendaka** subgen. **Kamendaka** Dist.

(35) (36) Lateral pronotal carinae not forming a prominent subfoliate ridge . . . . (37)

(36) (35) Lateral pronotal carinae forming a subfoliate ridge . . . . (41)

(37) (38) In profile vertex not ascending distad ; forming an even curve with frons . . . . **Nesocore** Kirk.

(38) (37) In profile vertex ascending distad . . . . (39)

(39) (40) In profile vertex ascending and curved backward **Nesoniphas** Kirk.

(40) (39) In profile vertex ascending, but not curved backward **Nesoneura** Kirk.

(41) (42) Subantennal process spatulate, attached to genae by a slender stalk . . . . (43)

(42) (41) Subantennal process not spatulate, attached to genae along a broad base . . . . (45)

(43) (44) Head in profile considerably produced beyond eyes ; antennae either small with large sensoria, or with second joint produced, bearing laminae so as to appear pectinate . **Kaha** Kirk.

(44) (43) Head in profile not much produced beyond eyes ; antennae moderately large with small sensoria . . . . **Nesokaha** Muir

(45) (46) Vertex truncate at apex ; lateral carinae of frons not contiguous, except rarely at middle of frons . . . . **Flaccia** Stål

(46) (45) Vertex acutely angulate, lateral carinae meeting at apex and remaining contiguous along frons to near apex . **Paralyricen** Muir

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[2] *Deribia* may run down to *Kuranda* or *Epotiocerus*, but as head characters in these genera are unreliable criteria it may well prove to be the same as *Leptaleocera*.

(47) (48) In profile vertex and frons forming a curve, not meeting angulately . . . . . **Makula** Dist.

(48) (47) In profile apex of head angulate . . . . . (49)

(49) (50) Tegmina with costal margin more or less sinuate and interrupted by an angular projection; a distinct precostal area in basal third . . . . . **Banksiella** Muir

(50) (49) Costal margin entire, not as above (see (31) above) . **Kamendaka** Dist.

(51) (52) A subantennal process present . . . . . **Neodendrokara** Muir

(52) (51) Subantennal process absent . . . . . (53)

(53) (54) Head in profile not much produced beyond eyes, apically rounded . . . . . **Dendrokara** Mel.

(54) (53) Head in profile considerably produced beyond eyes, apically narrowly rounded or angulate . . . . . (55)

(55) (56) Head in profile rounded at apex . . . . . **Shellenius** Ball

(56) (55) Head in profile angulate at apex . . . . . (57)

(57) (58) Head in profile notched near apex, beyond which apex angulately ascends . . . . . **Apache** Kirk.

(58) (57) Vertex in profile not notched, apex of head ascending in a curve **Otiocerus** Kby.

(59) (60) Head twice as long as pronotum and mesonotum combined **Vivaha** Dist.

(60) (59) Head relatively shorter . . . . . (61)

(61) (62) Subcostal cell short . . . . . (63)

(62) (61) Subcostal cell long; antennae cylindrical, sometimes complex (67)

(63) (64) Antennae large, laterally compressed . . . . . (65)

(64) (63) Antennae cylindrical . . . . . **Robigus** Dist.

(65) (66) Vertex little produced before eyes. Frons in profile parallel to margin of eye . . . . . **Leptaleocera** Muir

(66) (65) Vertex much produced before eyes; frons in profile almost oval **Epotiocerus** Mats.

(67) (68) Head in profile angulate or narrowly rounded apically, produced beyond eyes for more than width of an eye **Interamma** Wlk.

(68) (67) Head in profile apically forming a wide curve, not produced beyond eyes for more than width of an eye . . . . . (69)

(69) (70) Head with eyes as wide as pronotum or nearly so; vertex quadrate, wider at base than apex, distally truncate; lateral carinae of vertex and frons very large, not compressed together on frons . . . . . **Megatropis** Muir

(70) (69) Head with eyes narrower than pronotum; vertex triangular; lateral carinae of vertex and frons large, compressed together on frons . . . . . **Nicerta** Wlk.

(71) (72) Subantennal process present . . . . . **Mysidioides** Mats.

(72) (71) Subantennal process absent or very small . . . . . (73)

(73) (74) Antennae with first segment much longer than broad . . **Phra** Dist.

(74) (73) Antennae with first segment not longer than broad . . . . (75)

(75) (76) Antennae longer than frons . . . . . (77)

(76) (75) Antennae shorter than frons . . . . . (83)

(77) (78) Tegmina with Sc and R dilated at apex; vertex elongate, strongly ascending distally; mesonotum with a vertical flange-like lobe on line of each obsolete lateral carina **Anomaladerbe** Muir

(78) (77) Tegmina with Sc and R not dilated distally; vertex relatively short; mesonotum without vertical laminae on disc . . (79)

(79) (80) Frons in profile semicircularly rounded ; vertex not ascending . . . **Platonax** Metc.

(80) (79) Frons in profile shallowly convex ; vertex ascending distally, or very short . . . . (81)

(81) (82) Media in tegmen with four sectors ; vertex ascending distad, antennae flattened . . . . **Platocera** Muir[3]

(82) (81) Media in tegmen with five sectors ; vertex very short, not ascending, antennae cylindrical . . . . **Platocerella***

(83) (84) Antennae with second segment branched near base ; appendage curved ; frons at least as wide at base as at apex **Harpanor** Fenn.

(84) (83) Antennae with second segment cylindrical, devoid of appendage (85)

(85) (86) Vertex little produced beyond eyes ; frons distinctly wider at apex than at base . . . . (87)

(86) (85) Vertex markedly produced beyond eyes, frons compressed throughout, apex not wider than base . . . . . **Archara** Metc.

(87) (88) Subantennal process present ; ocelli present or indicated ; clypeus as long as frons . . . . **Heronax** subgen. **Heronax** Kirk.

(88) (87) No subantennal process ; ocelli absent ; clypeus two-thirds length of frons . . . . **Heronax** subgen. **Homometria***

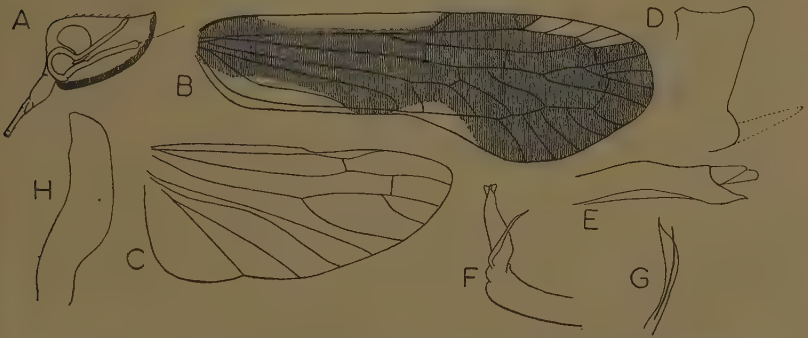

Fig. 27.—*Otiocerus regalis* sp. n. A, head, left side ; B, tegmen ; C, wing ; D, pygofer, left side ; E, anal segment of male, left side ; F, distal portion of aedeagus, right side ; G, flagellum of aedeagus, left side ; H, genital style, left side, side view.

Otiocerus Kirby.

Kirby, 1821 : 13, pl. 1, figs. 1–8. Logotype, *Otiocerus stollii* Kirby, 1821 : 16.

Otiocerus regalis sp. n. (fig. 27A–H).

Male : length, 5·0 mm. ; tegmen, 6·8 mm.

Head in profile subtriangular, slightly curved dorsad and acute at apex.

Pallid stramineous, powdered pallid, lateral margins of frons and a faint suffusion at apex of antennal process orange. Male genitalia lightly infuscate.

Tegmina bronzy-fuscous, distal portion of costal cell, apical cells of Sc and R, excluding nodal cell, two broadly crescentic areas, one in clavus, the other just distad of its apex, pallid. In life these areas are pale yellow and the infuscate area is purple. Wings hyaline, powdered greyish-white.

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[3] *Niphadodite* is apparently closely related to *Platocera*, but the vertex is produced almost as far as in *Anomaladerbe*.

Anal segment of male elongate, narrow, approximately parallel-sided, anal foramen near apex, lateroapical angles produced. Pygofer with laterodorsal angles subacutely rounded. Aedeagus long, narrowly tubular, shallowly curved, a spine on right side at base of flagellum, directed dorsad, two subequal spines on left side at base of flagellum; flagellum with two subparallel sclerotised rods from base to near apex, apical margin transversely bicuspidate. Genital styles in lateral view elongate, sinuate, of subequal width throughout, obliquely rounded-truncate distally.

Holotype, ♂, B.W.I.: St. Vincent, Morne Garu, 20.viii.1941, "taken on leaf of *Heliconia bihai*" (*R. G. Fennah*).

In shape of profile this species resembles *O. venustus* Fowler, but differs abundantly in coloration.

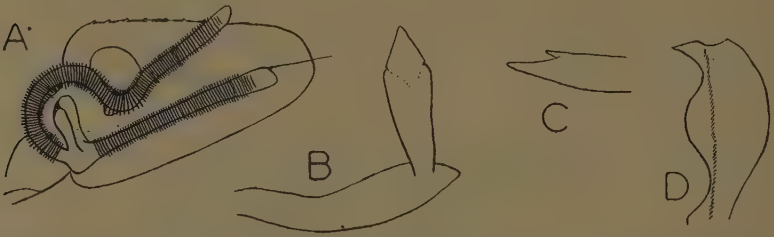

Fig. 28.—*Otiocerus fontis* sp. n. A, head, left side; B, aedeagus, right side, flagellum raised dorsad; C, apex of flagellum in profile; D, left genital style, side view.

Otiocerus fontis sp. n. (fig. 28A–D).

Male: length, 3·9 mm.; tegmen, 5·3 mm. *Female:* length, 4·1 mm.; tegmen, 6·2 mm.

Head in profile broadly rounded at apex, slightly concave on dorsal margin, apical margin only slightly surpassing antennae.

Pale stramineous, powdered white, margins of head at apex orange in male. Tegmina pale creamy-white, translucent, powdered white. Wings hyaline, powdered white.

Anal segment of male of moderate length, parallel-sided, porrect caudad, rounded-truncate at apex, not at all deflexed; anal foramen at apex, lateroapical angles not produced. Pygofer with laterodorsal angles obtusely rounded, not produced. Aedeagus tubular, unarmed, slightly curved upward distally; flagellum unornamented, slightly expanding distally, then tapering to a blunt point at apex, in profile slightly indented near apex. Genital styles in lateral view narrow, shallowly and evenly curved dorsad; in ventral view with a shallowly rounded eminence near middle.

Holotype, ♂, B.W.I.: St. Lucia, near Quilesse, "taken on dead leaf-bases of *Cyathea* at 1000 ft.," 22.iii.1939 (*R. G. Fennah*).

Paratype, 1 ♀, same particulars as holotype.

This species is distinguished by coloration and shape of genitalia.

Otiocerus lyncaeste sp. n. (fig. 29A–G).

Male: length, 4·0 mm.; tegmen, 5·5 mm.

Head in profile broadly rounded at apex; dorsal margin distinctly concave, apical margin markedly surpassing antennae.

Pale testaceous, head and abdomen pallid; lower margins of frons sparsely, a suffusion on antennae, a spot on pronotum behind eyes and on mesonotum near tegulae, orange. Tegmina translucent, faintly suffused dull yellow; medial portion of each cell, except at extreme base and in clavus, with a very pale fuscous suffusion. Wings hyaline, powdered white.

Anal segment of male of moderate length, apical margin abruptly deflexed; anal foramen at apex. Pygofer with latero-dorsal angles obtusely rounded, not produced. Aedeagus tubular, a pair of short curved spines distally at base of flagellum; flagellum tubular, shallowly sulcate in distal half, a short acuminate process near middle, a broadly lanceolate lobe arising near middle, directed towards apex, acute at its tip; flagellum bluntly pointed and slightly curved at apex. Genital styles in lateral view elongate narrow, of subequal width throughout, shallowly curved, in ventral view produced in a subtriangular eminence at middle of inner margin, sinuately transverse at apex.

Holotype, ♂, B.W.I.: Trinidad, Northern Range, St. John's Valley, 12.vi.1942 (*R. G. Fennah*).

This species is distinguished by the shape of the head and genitalia, and by coloration. In the shape of the profile this species resembles *O. griseus* Fowler, but differs very markedly in colouring.

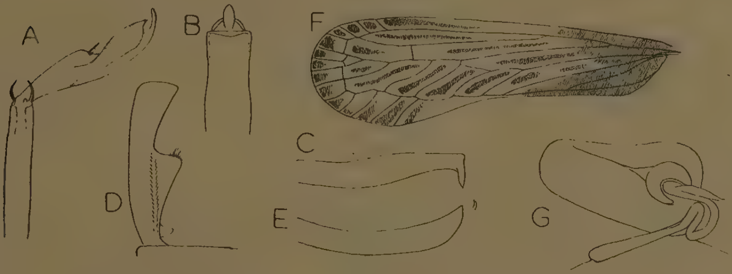

FIG. 29.—*Otiocerus lyncaeste* sp. n. A, aedeagus, ventral view with flagellum twisted laterocaudad; B, distal part of anal segment of male, dorsal view; C, anal segment of male, side view; D, left genital style, ventral view; E, left genital style, side view; F, tegmen; G, head, side view.

Anotia Kirby.

Kirby, 1821 : 20, pl. 1, figs. 9–11. Haplotype *Anotia bonnetii* Kirby, *ibid.*

Anotia sanguinea sp. n. (fig. 30A–E).

Male: length, 3·2 mm.; tegmen, 5·5 mm. *Female:* length, 3·5 mm.; tegmen, 6·5 mm.

Testaceous-yellow; antennae, sides of head, a broad band across pronotum behind eyes continued across mesonotum; middle line of mesonotum, pleurites and membrane of abdomen red. Abdominal tergites infuscate. Tegmina infuscate, two irregular spots in costal cell; a fascia from middle of tegmen in M to apex of clavus, a fascia from distal portion of costal margin to M in membrane, a marginal spot in apical cell Rs and a larger marginal spot in M, and a spot at distal third of clavus hyaline; veins red. Wings infuscate, a hyaline spot at forks of Cu.

Anal segment of male moderately short, lateroapical angles not produced, apical margin transverse. Pygofer with laterodorsal angles acutely produced. Aedeagus tubular, shallowly curved dorsad distally; flagellum relatively short and stout, submembranous throughout, with a rectangular sclerite on right side. Genital styles with mesoventral margin almost straight, dorsal margin with an auriculate process near middle.

Anal segment of female very short, distally rounded, broader than long. Pregenital sternite conically produced posteriorly. First valvulae of ovipositor with a subquadrate minutely denticulate lobe on inner face at base ; a series of five teeth on dorsal margin distally, the three distal teeth larger than basal two ; below this limb a submembranous lobe produced distally into two processes, one finger-like, the other subspinose ; second valvulae tapering and slightly deflexed distally with lower margin excavate two-thirds

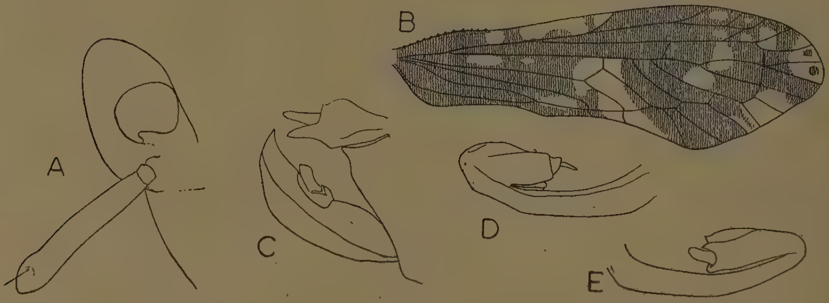

Fig. 30.—*Anotia sanguinea* sp. n. A, head and antenna, left side ; B, tegmen ; C, anal segment, posterior margin of pygofer and right genital style ; D, aedeagus, right side ; E, do., left side.

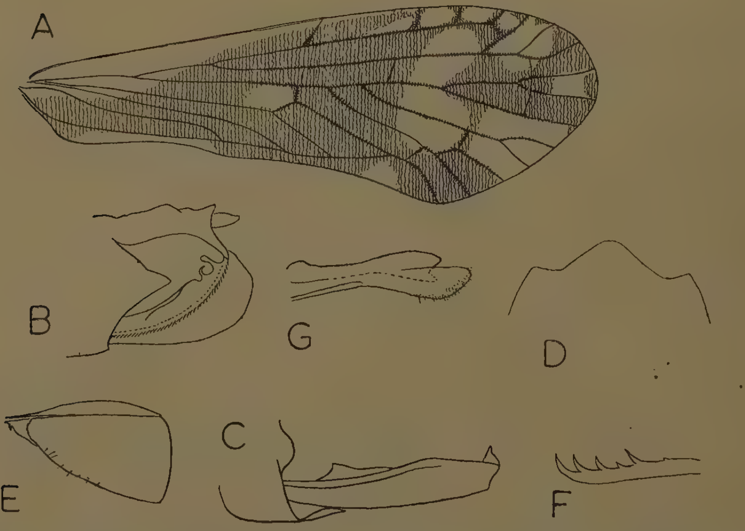

Fig. 31.—*Anotia fitchi trinitatis* subsp. n. A, tegmen ; B, anal segment, pygofer and left genital style ; C, right genital style and medioventral process, ventral view ; D, pregenital sternite of female ; E, third valvula of ovipositor, right side ; F, dorsal sclerite of first valvula of ovipositor ; G, second valvula of ovipositor, side view.

from base, a triangular lobe at base and a smaller triangular lobe on inner face one quarter from base; third valvulae comprising a narrowly triangular lobe dorsally and a more broadly triangular sclerite laterally, traversed by an oblique membranous furrow near apex. Bursa copulatrix beset with minute sclerotised rings with an irregular row of about seven large rings each bearing a short single spine, or two spines, at one side.

Holotype, ♀, B.W.I.: Trinidad, 18.xii.1928 (*J. G. Myers*) (B.M. 1929–170).

Paratypes, 9 ♂, 14 ♀, B.W.I.: Trinidad, La Reunion, Carapo, 14.ix.1949 (*R. G. Fennah*).

This species seems to be nearest to *A. venustula* Fowler, from which it differs in coloration.

Anotia fitchi Van Duzee.

Van Duzee, 1893 : 280.

Anotia fitchi trinitatis subsp. n. (fig. 31A–G).

Male: length 3·5 mm.; tegmen, 4·7 mm. *Female:* length, 3·4 mm.; tegmen, 5·8 mm.

Antennae of female distinctly shorter than in male. Apex of head in profile rounded, not subangulate.

Creamy-white, a suffusion on genae before lower margin of eyes, a broad stripe on each side of pronotum behind eyes, red, tinged with fuscous; a stripe on each side of mesonotum light fuscous, tinged with red; abdominal sclerites yellowish-fuscous, separated mediodorsally and at side by scarlet membrane. Antennae lightly infuscate with darker granules.

Tegmina mostly infuscate: a triangular area bounded by costal margin and a line from base of clavus to node, an area between M and Cu_{1b} at level of claval apex, a spot at apex of cell Sc, another in middle of subapical cell R, and a larger area immediately posterior to it in M, most apical cells except near margin, hyaline. Veins concolorous basally, becoming suffused with red distad, hyaline at apical margin. Wings lightly infuscate, veins rather darker. Male genitalia fuscous but anal segment pallid.

Anal segment of male moderately short, almost quadrate in dorsal view, latero-apical angles produced in a finger-like lobe directed ventrocaudad. Pygofer with dorsolateral angles strongly produced caudad to form an acute angle; medioventral process shallowly convex. Aedeagus with flagellum short, sclerotised on its dorsal surface in a quadrate plate produced distally in a slender spinose process on right, and in a similar but slightly stouter process on left. Genital styles moderately elongate, triangularly inflected apically; inner margin shallowly triangularly produced; in profile as figured.

Pregenital sternite of female as figured.

Holotype, ♂, B.W.I.: Trinidad, La Reunion, Carapo, "below leaves of 'wild tobacco,' *Acnistus arborescens*," 14.ix.1949 (*R. G. Fennah*).

Paratypes, 1 ♂, 3 ♀, same particulars as holotype.

This species is distinguished from *A. sanguinea* by its smaller size and more sober colouring. The antennae are shorter in both sexes, and are fuscous instead of scarlet, while the thoracic pleurites are pallid, not scarlet. The wing veins, and tegminal veins basally, are not red, as in *sanguinea*. The subspecies is distinguished by the wholly infuscate wings and the greater infuscation of the corium of the tegmen.

Anotia rubrinoda sp. n. (fig. 32A–D).

Male: length, 3·1 mm.; tegmen, 5·1 mm. *Female:* length, 3·5 mm.; tegmen, 5·2 mm.

Apex of head in profile bluntly conical, not broadly rounded; second antennal joint cylindrical, shallowly sinuate. Tegmina with Sc giving off 5 veinlets to margin, Sc with 3 apical veinlets.

Creamy-white, dorsal part of pronotum, mesonotum, and abdominal tergites pale golden yellow. Tegmina hyaline, a narrow diffuse fascia across basal third, another, following veins, from node to anal angle, most of claval area, all transverse veins, and a small round submarginal spot in apical cells, lightly infuscate; veinlets between Sc and anterior margin red, the basal veinlet both black and red, veins otherwise pale stramineous. Wings hyaline, veins pallid stramineous with exception of R–M crossvein, which is infuscate. Insect powdered white.

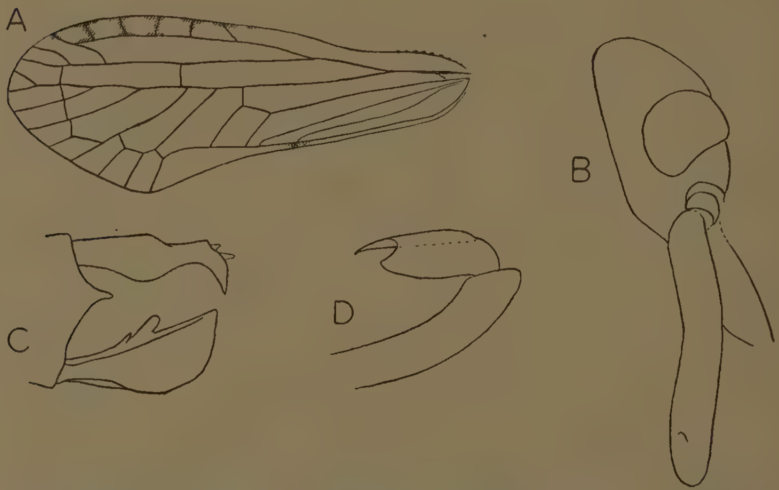

Fig. 32.—*Anotia rubrinoda* sp. n. A, tegmen; B, head, right side; C, anal segment, posterior margin of pygofer, and left genital style; D, aedeagus, left side.

Anal segment of male about as long as genital styles; lateral margin sinuate in profile, strongly decurved at apex; anal foramen near apex. Pygofer with laterodorsal angles produced in a short narrow lobe. Aedeagus tubular, shallowly curved; flagellum about half as long as aedeagus dorsally, dorsally convex, hollowed out below, distally bluntly lobate on left side and acuminate on right. Genital styles as figured.

Holotype, ♂, B.W.I.: Trinidad, La Reunion, "resting on leaves of 'wild tobacco,' *Acnistus arborescens*," 16.vii.1949 (*R. G. Fennah*).

Paratypes, 8 ♂, 11 ♀, same particulars as holotype.

This species appears to be nearest to *Anotia tenella* Fowler in colouring, but differs in the distal venation of Sc, in which it approaches *Anotia smithi* Fowler, from which, in turn, and from *Anotia invalida* Fowler, it is separated by its colour pattern.

Anotia formaster sp. n. (fig. 33A–J).

Male: length, 3·4 mm.; tegmen, 5·7 mm. *Female:* length, 4·4 mm.; tegmen, 6·3 mm.

Head in profile produced ascendingly before eyes, apex acute. Antennae cylindrical, in male scarcely surpassing apex of head, in female shorter, arista subterminal. Costal margin of tegmina produced at base in a shallow reflexed lobe.

Vertex and genae translucent white; middle line of vertex, and frons, a curved line between lower margin of eye and frontoclypeal suture, and antennae, scarlet; clypeus scarlet suffused fuscous medially; subapical joint of rostrum white, apical joint fuscous; pronotal disc, tegulae, and mesonotum except mesoscutellum orange with slight fuscous suffusion; pronotum red behind eyes; ventrally and posterolaterally white; base of procoxae, mesepimera and metepimera, mesoscutellum and metanotum, meso- and metatibiae and tarsi, abdominal tergites narrowly along anterior and posterior edges, anal styles and tip of lateral process on pygofer, white; other parts of legs, mesepisterna and

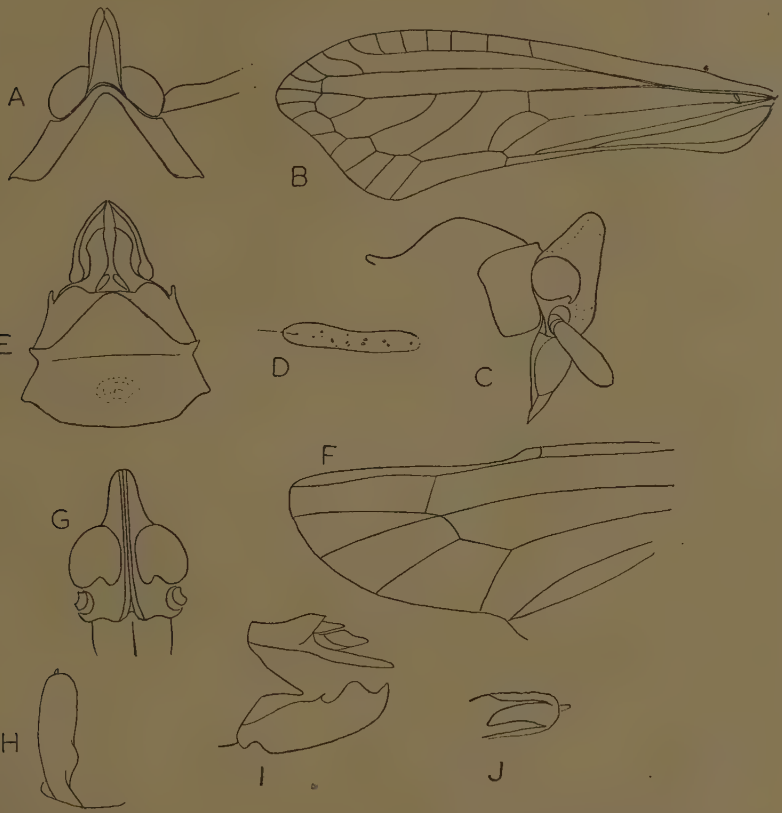

FIG. 33.—*Anotia formaster* sp. n. A, head and pronotum, dorsal view; B, tegmen; C, head and pronotum and mesonotum, side view; D, antenna; E, female genitalia, ventral view; F, distal part of wing; G, frons, anterior view; H, left genital style, ventral view; I, anal segment, posterior margin of pygofer and left genital style; J, flagellum of aedeagus, right side.

metepisterna, membrane of abdomen, anal segment, and a suffusion over male genitalia, scarlet; abdominal sclerites and male genitalia otherwise fuscous.

Tegmina mostly deeply infuscate; costal margin, most of costal cell near base, a triangular area on hind margin just distad of apex of clavus, extending inward to middle, yellowish-hyaline; interval areas along distal part of anterior margin, and a spot at junction of each apical veinlet with margin, white; veins in fuscous areas scarlet, in yellow areas concolorous. Wings fuscous except for a yellowish-hyaline marginal area in Cu; veins and stridulatory area scarlet.

Anal segment of male moderately short, latero-apical angles strongly produced with narrow processes; mediodorsally a small blunt tooth. Pygofer with laterodorsal angles strongly produced caudad in an acutely triangular process; medioventral process absent. Aedeagus ventrally with a single longitudinal carina close to middle line with a small narrow triangular depression at its base; flagellum short, thick and fleshy, a small fuscous scoop-like semicircular sclerite medially at apex, lying at bottom of a broad shallow depression; left side of flagellum sclerotised but unarmed, right side with a stout adpressed spine dorsally, and a broader adpressed spine below it, both directed cephalad.

Pregenital sternite of female as figured.

Holotype, ♂, B.W.I.: Trinidad, La Reunion, Carapo, "taken below leaves of 'wild tobacco,' *Acnistus arborescens*," 14.ix.1949 (*R. G. Fennah*).

Paratypes, 3 ♀, same particulars as holotype.

This species is distinguished from *A. sanguinea*, to which, of Trinidad species, it bears closest general resemblance, by the acutely angulate profile of the head, by the shorter antennae and by the shape of the tegmina.

Cobacella gen. n.

Vertex about twice as long as broad across base; posterior margin excavate, lateral margins converging distally; disc depressed, in profile moderately produced before eyes, rounding into frons; genae without subantennal process; antennae subcylindrical, shorter than head. Pronotum short medially, medially carinate; mesonotum relatively large, about as broad as long; posterior margin of mesoscutellum transverse, ecarinate. Tegmina widest three-fifths from base, apical margin deeply rounded; Sc + R fork about one-fifth from base, M arising from basal cell or very nearly so, Cu_1 forked near level of union of claval veins; apical areoles at least twice as long as broad; clavus extending for a little more than one-third of length of whole tegmen.

Anal segment of male short, anal foramen near apex, apical angles shortly produced lateroventrad. Pygofer devoid of medioventral process.

Type species, *Otiocerus* (?) *rubescens* Fowler, 1900 : 76, pl. 9, fig. 2.

This genus differs from *Otiocerus* and *Anotia* by characters given in the key. In the field it is unmistakably distinguished when at rest by the carriage of the tegmina, which are directed laterocaudally with the apical portion touching the substrate, or nearly so. *Anotia* characteristically directs the tegmina steeply upward and slightly outward, and thus assumes a V-shape when viewed from front or rear.

Cobacella sexguttata sp. n. (fig. 34C–I).

Male: length, 6·0 mm.; tegmen, 8·3 mm. *Female:* length, 5·5 mm.; tegmen, 8·8 mm.

Ivory-white; lateral margins of vertex, frons and anterior portion of genae, middle line of clypeus, sometimes profemora and mesofemora at base and apex, and protibiae at apex, anal segment of male, ventral surface of pygofer, and a suffusion on genital styles, orange-red; six round spots on latero-caudad margins of mesonotum piceous, abdominal tergites fuscous. Tegmina translucent, dull yellow, a suffusion at base and across apical portion of membrane fuscous; veins concolorous except at apex and Sc and claval veins at base, where, like the costal and apical margin, they are scarlet-red. Wings hyaline, suffused with fuscous at base and apex.

Anal segment of male short, almost as broad across apex as long in middle line; latero-apical angles acute and diverging. Aedeagus asymmetrical, sinuately tubular; flagellum with a single spinose process at its base, and a flattened plate, acute at tip, on left; on right two sclerites, distally acute, supporting membranous portion. Genital styles narrow in profile, curved dorsad distally, broadly sulcate longitudinally in distal three-quarters, a small spine near middle dorsally, directed latero-caudad, and a subconical setose eminence on inner face near base.

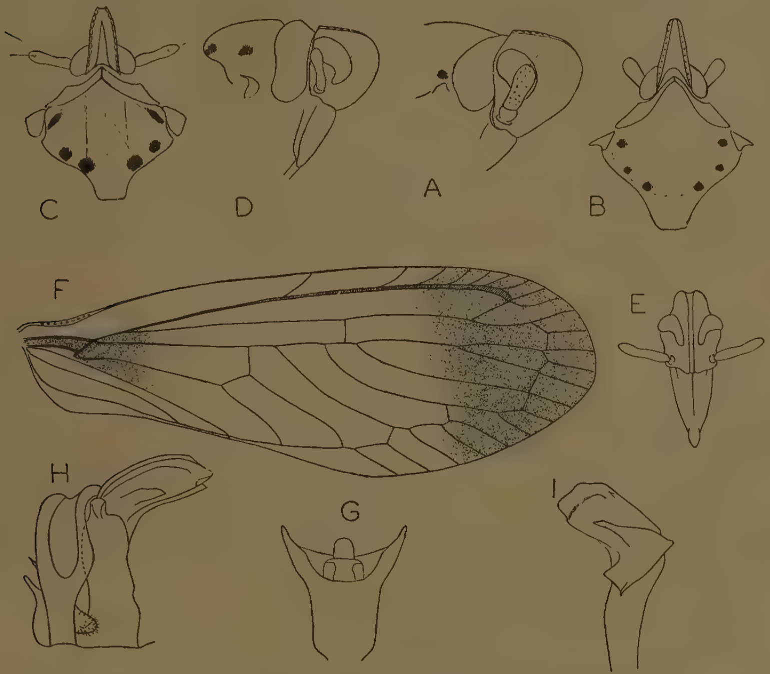

Fig. 34.—*Cobacella rubescens* (Fowl.). A, head and pronotum, side view; B, head and thorax, dorsal view.

Cobacella sexguttata sp. n. C, head and thorax, dorsal view; D, head and pronotum, side view; E, head, anterior view; F, tegmen; G, anal segment of male, dorsal view; H, left genital style and aedeagus, ventral view; I, aedeagus, dorso-lateral view, right side, flagellum raised.

Holotype, ♂, B.W.I.: Trinidad, La Reunion, Carapo, "resting on leaves of 'wild tobacco,' *Acnistus arborescens*," 14.ix.1949 (*R. G. Fennah*).

Paratype, 1 ♀, same particulars as holotype.

This species is close to *Cobacella rubescens* Fowler (fig. 34A, B), but the vertex is not produced so far before the eyes. The coloration is different, while the bodily size is substantially greater than that of *C. rubescens*. The figures of the type of *C. rubescens* Fowler have been kindly provided by Dr. W. E. China.

Platocerella gen. n.

Vertex small, triangular; lateral margins of frons contiguous, in profile more or less following anterior margin of eyes, convex but not deeply so, only slightly indented at frontoclypeal suture; eyes reniform, not deeply excavate; antennae with basal joint short, second joint surpassing anterior margin of head, approximately cylindrical, third joint inserted apically. Pronotum narrow medially, relatively broad laterally, posterior margin angulately excavate; mesonotum moderately convex. Tegmina narrow basally, moderately dilated distally. R separating from M at level of apex of clavus, typically with three veinlets at margin; M five-branched with first and fourth branches forked at transverse line of cross-veins; Cu_1 two-branched, with anterior branch fused with last branch of M for a short distance.

Anal segment of male elongate, narrow, anal foramen in profile situated at middle. Pygofer with laterodorsal angles more or less angulately produced, medioventral process present, distally acute. Genital styles rather elongate, subspatulate, a shallow lobe dorsally near base, bearing a brush-like series of minute setae and a short stout curved spine.

Type species, *Platocera rubicundum* Muir.

This genus differs from *Platocera annulipes* Muir, the type species of *Platocera*, in that the lateral margins of the frons are close to, and follow the curve of, the anterior margin of the eyes, instead of being strongly produced before them, in the antennae being cylindrical and relatively shorter, and in tegminal venation. From *Platonax* Metcalf it differs in profile of frons (which in *Platonax* is almost semicircular) and in shape of antennae; in external male genitalia *Platocerella* differs from *Platonax* in the shape of the laterodorsal angles of the pygofer, which are not at all produced in *Platonax*, and in the general shape of the genital styles, especially in the deeply rounded apical margin as contrasted with the obliquely truncate apical margin of *Platonax*. These two genera, however, are probably rather closely allied.

Platocerella rubicunda (Muir) (fig. 35A–F).

Platocera rubicundum Muir, 1918 : 421.

Male: length, 4 mm.; tegmen, 8·5 mm.

Fuscous, with red suffusion; carinae of frons, rostrum, lower side of thorax and legs stramineous. Tegmina fuscous, costal margin and distal portion of costal cell except at node, an area at apical angle, another at middle of apical margin, a small spot near R + M fork, another just basad of Cu fork and about four spots anteriorly in M, and a lenticular area between margin and M_4 hyaline, powdered white; clavus between anterior vein and sutural margin testaceous; veins in anterior part of tegmen and apical margin crimson red, elsewhere concolorous. Wings slightly smoky, an area in Cu at margin translucent, pallid, veins red.

Anal segment elongate, narrow, latero-apical angles produced and deflexed through 105°. Pygofer rather narrow, laterodorsal angle rectangulate, posterior margin oblique with an eminence near middle, medioventral process pointed. Aedeagus tubular, curved, with a pair of spinose processes distally at point of insertion of flagellum; flagellum with two narrow lobes at base, a sinuate spine on left side near base, a broad membranous lobe distad of this, tapering abruptly to a short spine; a long slender process on dorsal margin, distally subtruncate and on right side a stout pigmented spine with a semi-detached supporting rod below; upper surface of flagellum more or less sclerotised. Genital styles rather elongate, subspatulate in profile; dorsal margin bearing a brush-like series of minute setae and a short, stout curved spine on an eminence near middle, a small triangular process near apex, apical margin deeply rounded.

Redescribed from 1 ♂ (H.2972) from BRITISH GUIANA: Pakaraima Mountains, Upper Ireng River, 1932 (*J. G. Myers*) (B.M. 1933–400).

Sayiana Ball.

Ball, 1928 : 197. Orthotype, *Anotia sayi* Ball, 1902 : 259.

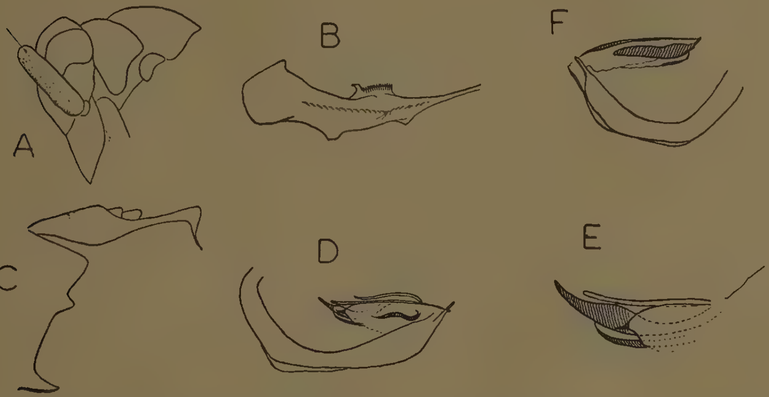

FIG. 35.—*Platocerella rubicunda* (Muir). A, head and pronotum, side view; B, right genital style; C, anal segment and posterior margin of pygofer, side view; D, aedeagus, left side; E, apex of flagellum, left side; F, aedeagus, right side.

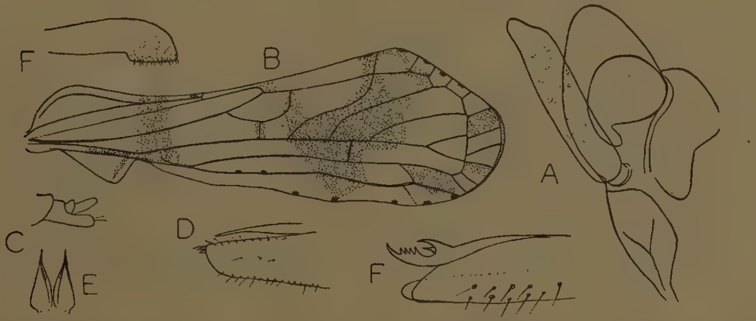

FIG. 36.—*Sayiana maracasa* sp. n. A, head and pronotum, side view; B, tegmen; C, anal segment of female, side view; D, third valvula of ovipositor, right side; E, dorsal lobes of third valvulae, dorsal view; F, first valvula of ovipositor, right side.

Sayiana maracasa sp. n. (fig. 36A–F).

Female: length, 2·7 mm.; tegmen, 4·2 mm.

Stramineous; a broken line between pustules outside lateral carinae of frons, a stripe on side of head above eyes, antennae, apex of rostrum, tarsi, femora at apex, a spot near base of Cu in wing, red or fuscous. Tegmina translucent, a suffusion in basal quarter and another between Sc and sutural angle pale fuscous; distal portion of Sc and base of Sc orange.

Anal segment of female short. Pregenital sternite triangular. First valvulae of ovipositor comprising a ventral sparsely setiferous lobe and a dorsal sclerotised limb bearing seven teeth, with the basal two and the apical tooth larger than intervening four; second valvulae moderately narrow, ventral margin straight, dorsal margin decurved in distal half; third valvulae moderately elongate with dorsal and ventral margins straight, tapering distally, each with a membranous triangular lobe dorsomesally. Vagina devoid of sclerites, bursa copulatrix densely beset with thick-walled rings.

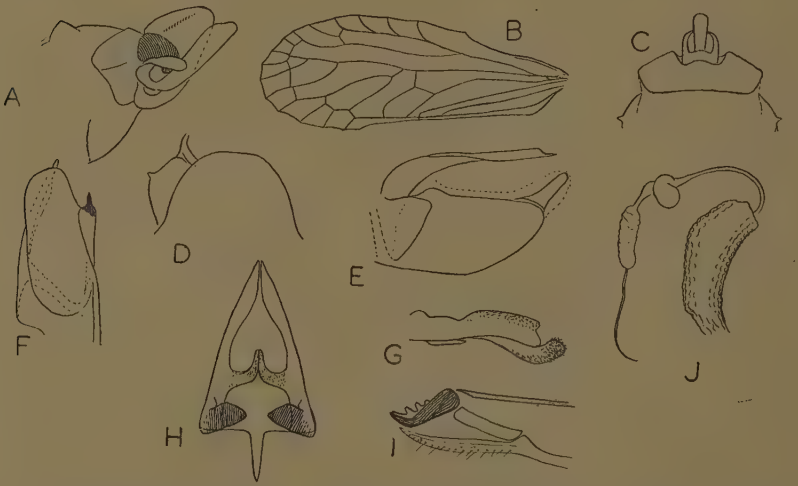

Fig. 37.—*Iquitosa scalprata* sp. n. A, head and thorax, side view; B, tegmen; C, eighth segment and anal segment of female, dorsal view; D, pregenital sternite and lateral sclerite of left side of eighth segment; E, third valvula of ovipositor, left side; F, do., dorsal view; G, second valvula of ovipositor, left side; H, second valvula of ovipositor, ventral view; I, first valvula of ovipositor, right side; J, spermatheca.

Holotype, ♀, B.W.I.: Trinidad, Maracas, "on coconut," 2.vii.1924 (*C. L. Withycombe*) (B.M. 1924–383).

This species differs markedly from the typical species in shape of antenna, the simple venation of Sc and R and in the size and shape of the basicostal eminence in the tegmina. The wings have R simple, M and Cu_1 each forked once.

Iquitosa Fennah.

Fennah, 1945*a*: 101. Orthotype *Iquitosa shannoni* Fennah, *ibid.*, pl. 2, figs. 23–26; pl. 3, figs. 39–41.

Iquitosa scalprata sp. n. (fig. 37A–J).

Female : length, 3·2 mm. ; tegmen, 5·0 mm.

Form as in typical species. Antennal appendage shorter than second segment, curved outward and forward. Stramineous ; sides of head above posterior margin of eyes, and anteroventrally before eyes, clypeus, except in middle part of median carina, apex of rostrum, femora suffusedly, a transverse band across middle of pro- and mesotibiae, and basal half of post-tibiae, pro- and mesotarsi, fuscous ; lateral areas of pronotum except margins, mesonotum except carinae and a triangular area from eminences to postero-lateral margin, thoracic pleurites, reddish-brown. Tegmina pearly-translucent, powdered pallid ; basally, including costal appendage, fuscous interrupted with pallid spots, elsewhere very sparsely lightly suffused fuscous as figured, costal margin between apical veinlets of Sc spotted red. Wings pearly, powdered white.

Anal segment of female short, broader than long. Pregenital sternite broadly and semicircularly rounded ; lateral sclerites of eighth segment each bearing a pointed tubercle at middle. First valvulae each with a stout V-shaped pigmented lobe attached at base terminating in a thick short curved plate with five short blunt teeth on apical margin ; second valvulae with a short triangular lobe on each side basally, directed mesad, a narrow setose lobe near middle of each limb, directed caudad, apex in profile as figured ; third valvulae longer than broad (1·6 : 1), apical margin oblique, produced at dorsal angle in a blunt process ; dorsal lobe of valvulae distally twisted and acuminate ; vagina with a large sabot-shaped sclerite in its ventral wall, and a small rounded sclerite on its left side ; wall of vagina thickened opposite entrance of spermatheca ; entrance to bursa copulatrix armed with two very small sclerites, one bearing a distinct short peg-like process, the other similar but its process obsolete.

Holotype, ♀, B.W.I. : Trinidad, 1939 (*A. M. Adamson*).

The present species differs from *I. shannoni* in the rather less acute profile of the head, in the relatively longer and much more widely curved antennal appendage, in the triangular shape of the mesonotal eminences, in tegminal venation (first and second sectors of M—veins M_3 and M_4—being united basally in a short common stalk), and in coloration.

As *I. shannoni* was taken in Peru, it would appear from the above record that the genus is widespread in the northern part of South America.

Heronax Kirkaldy.

Kirkaldy, 1906 : 431. Orthotype, *Heronax parnassius* Kirkaldy, *loc. cit.*

Homometria subgen. n.

Vertex triangular, little produced beyond eyes, apex in profile subangulate ; rostrum with apical joint about half as long as subapical ; genae without a subantennal process ; ocelli absent ; antennae less than three-quarters of length of frons, with first segment short, not longer than broad ; second segment short, cylindrical, narrower medially, devoid of appendages. Pronotum medially short, carinate, laterally broad ; posterior margin angulately excavate, a sinuate carina at lateral margin behind eye.

Tegminal venation as in *Heronax.*

Type species, *Mysidia elatior* Fowler.

Homometria elatior (Fowler) (fig. 38).

Mysidia elatior Fowler, 1900 : 73, pl. 8, fig. 22.

The figure was prepared by Dr. China from the female type. This subgenus differs from Old World *Heronax* in the absence of a subantennal process and of all trace of ocelli; in the long apical rostral segment (which is less than twice as long as broad in the typical subgenus), and in the relative lengths of clypeus and frons. In profile the clypeus of *Heronax* measured from apex of labrum to frontoclypeal suture is as long as the distance from the suture to the margin of the vertex above the eye: in *Homometria* the clypeus, similarly measured, is only two-thirds of the length of the frons.

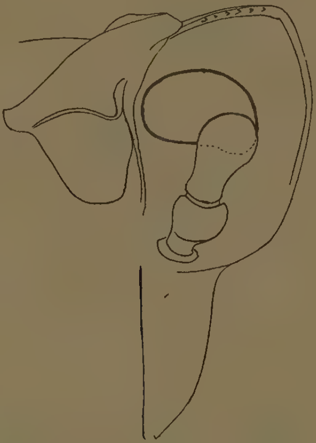

Fig. 38.—*Heronax* (*Homometria*) *elatior* (Fowl.). Head and pronotum, side view.

TRIBE RHOTANINI.

The writer is not wholly satisfied with current generic concepts in this tribe, but considers that a critical study can only be made on adequate series from the Orient and the Pacific.

The following key is offered as an alternative to that of Muir (1918 : 231); both have been constructed with the aid of relatively weak characters.

Muir has suppressed *Alara* Distant under *Levu* Kirkaldy without accounting for the discrepancies. On this basis other synonymy would appear equally justifiable, and until a critical review is possible the writer considers it preferable to keep these concepts apart.

Key to Genera of Rhotanini.

(1) (2) Tegmina not more than twice as long as broad, usually less . . . (3)
(2) (1) Tegmina at least twice as long as broad . . . . (5)
(3) (4) Frons with lateral carinae not at all contiguous . . **Decora** Damm.
(4) (3) Frons with lateral carinae contiguous at least basally. . **Rhotana** Wlk.
(5) (6) Second antennal segment at least twice as long as broad . . . (7)
(6) (5) Second antennal segment little longer than broad . . . **Levu** Kirk.
(7) (8) Second antennal segment robust, tumid, more than twice as long as broad; frons not strongly compressed distally. Base of M and Cu widely separated . . . . **Alara** Dist.
(8) (7) Second antennal segment not exceptionally large, barely twice as long as broad; frons compressed throughout. M and Cu branching together from Sc + R . . . . **Sumangala** Dist.

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STUDIES ON THE REPRODUCTIVE CYCLE OF THREE SPECIES OF BRITISH HETEROPTERA, WITH SPECIAL REFERENCE TO THE OVERWINTERING STAGES.

By T. E. Woodward, M.Sc.(N.Z.), Ph.D.(Lond.), D.I.C., F.R.E.S.

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With 15 Text-figures.

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I. INTRODUCTION.

THE species dealt with in this paper are the Mirids *Stenodema laevigatum* (L.) and *Notostira erratica* (L.) and the Coreid *Myrmus miriformis* (Fallén). In a preliminary section is presented a classification of the types of reproductive cycle met with in the Heteroptera and the three species concerned are relegated to their places in this scheme. The investigations were concentrated mainly on the overwintering stages, viz., the adults in *S. laevigatum* and *N. erratica* and the eggs in *M. miriformis*, and on the nature of the resumption of development in each insect after hibernation. It is realised that they have raised more problems than they solve but, as the writer is not likely to be able to do additional work on these species, the results are given as they stand and indications are made of further desirable lines of research. For classification and and nomenclature China (1943) has been followed.

II. THE REPRODUCTIVE CYCLE IN THE HETEROPTERA.

The following classification is proposed as one which seems to include conveniently the main types of reproductive cycle encountered in this sub-order.

I. *Species in which Oviposition is more or less Continuous throughout the year.*

(1) Species with long-lived adults (about a year); univoltine or with the successive generations widely overlapping: e.g., *Notonecta glauca* L., which oviposits in winter as well as at other times of the year, both adults and eggs thus overwintering (Butler, 1923). There is apparently no cessation of ovarian development during the colder months. The comparatively uniform temperature conditions of the aquatic environment are no doubt important in permitting such continuous reproductive activity.

(2) Bi- or multi-voltine species with comparatively short-lived adults, with ovarian development and oviposition continuing during winter.

Probably very few British Heteroptera are of this type, though the records indicate that possibly some of the Aradidae and Brachyrhynchidae, which live in protected situations, may be included here. A reproductive cycle of this kind is to be expected more commonly in tropical and sub-tropical forms.

II. *Species in which Oviposition is Restricted to the warmer parts of the year.*

(1) Species with long-lived, overwintering adults (at least in one generation).

(a) Univoltine species which oviposit in spring and/or summer. In this group are included the British Cydnidae, Naucoridae, Nepidae, most Pentatomidae and Corixidae, and about half of the Nabidae, together with many species of other families (e.g., a few Mirids, including *Stenodema laevigatum*, dealt with in this paper).

(*b*) Bi- or multi-voltine species with the adults of the early generation or generations comparatively short-lived and those of the autumn, overwintering generation long-lived and ovipositing the following spring; e.g., a few bivoltine species of British Miridae: *Notostira erratica* (L.) (Kullenberg, 1944, and present work) and *Chlamydatus evanescens* (Boh.) (Kullenberg, 1944). The Mirid *Lygus pratensis* (L.), which usually overwinters as an adult, is also probably bivoltine in England (Theobald, 1905; Fox-Wilson, 1925; Austin, 1931; *et al.*). In *N. erratica* only the females overwinter, in the other species both sexes. Among other Heteroptera included in this group are *Cimex lectularius* L. (Cimicidae), and probably also, according to Butler (1923), *Cryptostemma alienum* (H.-S.) (Cryptostemmatidae (Dipsocoridae)), *Microvelia reticulata* (Burm.) (Veliidae), *Chartoscirta cocksi* (Curtis) (Saldidae), and *Cymatia coleoptrata* (Fabr.) and *Micronecta minutissima* (L.) (Corixidae).

(2) Species with comparatively short-lived adults; hibernation in egg stage.

(*a*) Univoltine species; e.g., most British Miridae, about half of the species of Nabidae, and the two Coreids *Myrmus miriformis* (Fallén) and *Chorosoma schillingi* (Schummel) Schilling.

(*b*) Bi- or multi-voltine species; e.g., the following British species of Miridae: *Lygus pabulinus* (L.) (Petherbridge and Thorpe, 1928), *Orthotylus flavosparsus* (C. Sahlberg) and *Chlamydatus pullus* (Reuter) (Kullenberg, 1944), probably also *Calocoris norvegicus* (Gmel.) (Smith, 1931).

These main types of reproductive cycle form a series in respect to the extent of inhibition of ovarian development by winter conditions. In Class I there is no interruption of egg production during winter, or, at the most, a slowing down of ovarian maturation. In Class II (1) either the production of egg rudiments is completely inhibited until spring or their development is interrupted or considerably retarded during winter; e.g., in *Stenodema laevigatum* and *S. calcarata* (Miridae), and in *Piezodorus lituratus* (Pentatomidae) no egg rudiments are formed until spring, whereas in *Notostira erratica* (Miridae), the overwintering species of *Nabis* (Nabidae), and *Scolopostethus decoratus* (Lygaeidae), the formation of small egg rudiments begins in autumn, but is arrested by the adverse conditions of winter (present paper and Woodward, 1949). In either case, formation and laying of ripe eggs is delayed until spring. In Class II (2) not only is sexual development and oviposition restricted to the warmer months, but, in addition, none of the adults survive the winter.

The essential differences between these three classes are expressed diagrammatically below (fig. 1), in each case with the possible interpolation of one or more additional generations understood. The horizontal lines indicate the seasonal occurrence of adults and the arrows times of oviposition.

Dick (1937) listed the following types of oviposition cycle found in the Coleoptera:

(1) Species which live only a short time as adults and lay all their eggs within a few days.

(2) Species which live for a long time—often over a year—as adults and produce eggs continuously over a long period.

(3) Species which, during one season, lay eggs in batches at fairly short intervals of time.

(4) Species which lay more or less continuously in two or more seasons, separated by a period during which oviposition ceases.

It is doubtful whether any British Heteroptera, except possibly some of the short-lived Mirids, could be referred to Dick's first type. To the second type would belong a few long-lived bugs such as *Notonecta glauca.* Almost all British Heteroptera would be included in the third class. There seem to be no recorded examples of the fourth type of cycle; so far as is known, all Heteroptera which hibernate as adults do so before producing ripe eggs.

Although most species conform to one or other of the types of cycle here proposed, there are a few species in which some individuals follow one course of sexual development and others a different course. For example, the Mirid *Lygus pratensis* (L.) usually overwinters as an adult (Class II (1*b*)), but occasionally in the egg stage (Class II (2*b*)) (Theobald, 1905; Miles, 1928). As indicated above, some families display mainly or entirely one type of cycle in Britain, while in others the different members follow two or more different lines of development. Thus the classification is one of convenience, with no wide phylogenetic significance. This is to be expected when due consideration is given to the extreme variability and adaptation shown by insects in their reproductive behaviour. In some species this adaptation (to differences in climatic and other conditions) is apparently mainly hereditarily determined, while in others it seems that environmental variations can act directly on individuals in modifying the nature of the reproductive cycle. But little seems to be known in the Heteroptera of the relative importance of the genetic and environmental factors in determining voltinism and the stages at which overwintering occurs.

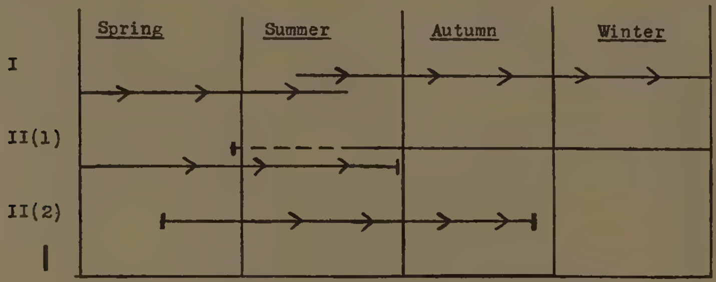


Fig. 1.—The main types of reproductive cycle in the Heteroptera.

Two British species of Pentatomidae are known to hibernate as nymphs —*Odontoscelis dorsalis* (Fabr.) (Butler, 1923) and *Pentatoma rufipes* (L.) (Walker, 1917; Butler, 1923)—while in a few other species of Heteroptera the seasonal distribution of instars indicates overwintering in both nymphal and adult stages, e.g., *Aneurus laevis* (Fabr.) (Brachyrhynchidae) (Butler, 1923), *Aradus depressus* (Fabr.) (Aradidae), *Acalypta carinata* (Panzer) (Tingitidae) (Butler, 1923), *Aepophilus bonnairei* Sign. (Aepophilidae).

III. The Reproductive Cycle in *Stenodema laevigatum* (L.)

(1) *Outline of Life-cycle.*

S. laevigatum, a Mirid which feeds on the leaves and inflorescences of grasses, is a univoltine species overwintering as adults in both sexes. Emergence of adults begins early in July and continues throughout this month and August.

A period of intensive feeding ensues during which a large fat-body is laid down in both sexes. With the onset of colder weather the insects retire to the bases of large grass-tufts and remain there in a more or less inactive condition during the winter. When disturbed in cold weather they are very sluggish, but if removed from their hibernation quarters to higher temperatures quickly become active again. A colour change, much more complete than occurs in *Notostira erratica* (Section IV (1)), is undergone by the overwintered bugs. Whereas before hibernation the adults are ochreous, by late spring their colour has changed to an intense grass-green. Sexual activity is delayed until spring, when copulation occurs and the first egg rudiments are formed. Oviposition begins during the second half of May and continues until the end of June, although a few females may remain alive during July. There is thus a period of overlap of nearly a month when some females of both the overwintered and the new generations may occur in the field together. The males die off earlier than the females, after the copulation period, becoming scarcer in the second half of May and none being found by the end of June. In the spring, with sexual maturation and the general renewal of activity, there is rapid depletion of the fat-body. Adult life is long in both sexes, with a maximum length of about 12 months in the females and in the males about a month less. Eggs are laid between the glume and lemna of grass spikelets (Kullenberg, 1944), and hatch after an incubation period of about a fortnight (Butler, 1911). Emergence of nymphs takes place in June and July. The nymphal instars are passed through in about 30 days; this figure agrees with the time taken for development by a single specimen reared by Butler (1911) and with data on the appearance of nymphs and adults in the field.

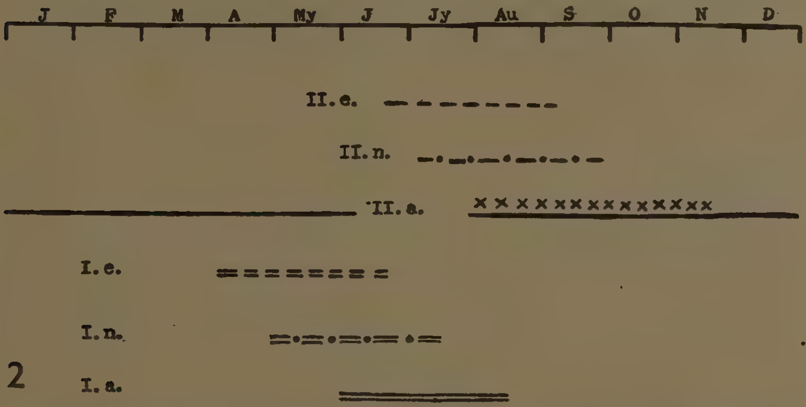


FIG. 2.—Seasonal distribution of eggs, nymphs, and adults in the two generations of *Notostira erratica* (L.). *e*, eggs; *n*, nymphs; *a*, adults; I, first generation; II, second generation. × indicates occurrence of second generation males.

Butler (1923), who gave adult records for February to October, noticed only females during spring and supposed that copulation occurred in autumn, the males then dying, although, since he had taken an occasional male in February, he considered spring fertilisation also a possibility. During the present investigations in southern England (at Slough, Bucks.; Sunninghill, Berks.; and Putney Heath, London), both sexes in approximately equal numbers (66 females, 73 males), were found in hibernation from November to February, and in spring were found abundantly until about the middle of May (183 females, 122 males). After this time the males became scarcer, only occasional specimens being caught in the second half of May and the first half of June (17 males as against 364 females). No males were found later than 12.vi.47. The overwintered females remained abundant throughout May and most of June, becoming considerably reduced in numbers by the last week of this month. None were found later that 3.vii.47. In dissected females the occurrence of fertilisation is readily detected by the turgid yellow appearance of the sperm–filled bursa copulatrix, a thin-walled sac opening into the anterior end of the common oviduct (fig. 3). No females were seen to be fertilised in the autumn; copulation seems invariably to be delayed until early May.

As Kullenberg (1944) found in Sweden, both nymphs and adults of *S. laevigatum* seem to prefer as food the young seed-heads of grasses. In captivity they were seen to concentrate on the inflorescences of *Sieglingia* (*Triodia*) *decumbens* when fresh leaves were also available. In the field the adults were observed feeding on the seed-heads of species of *Agrostis*.

(2) *Sexual Maturation.*

(a) *Females.*

No egg rudiments are formed before or during hibernation. Instead, a process of complete "gonotrophic dissociation" ensues, with the laying down of a large fat-body in autumn. This is accompanied by a considerable reduction in water content and an increase in body weight. Details of this process are given in Section V (3), where a comparison is made with *Notostira erratica* and the conclusion reached that in *Stenodema* (though not in *Notostira*) there is an obligatory arrest or diapause in ovarian development which must be broken before the higher temperatures of spring can induce egg formation.

Egg rudiments begin to form early in April, more or less concomitant with release from hibernation and the resumption of active movement and feeding. By this time, together with a reduction in size of fat-body, the body weight has also fallen. By 10.iv.47 the average for 32 specimens was 6·4 mg. (5·0–7·0 mg.). This is the same weight as near the beginning of adult life (average of 87 females on 25.vii.47), and contrasts with that at the end of the prehibernation feeding period (average of 7·3 mg. on 5.ix.47 for 37 females). As in other Heteroptera, each egg rudiment first appears as an opaque region at the base of the germarium, from which it soon becomes separated by a constriction. By 10.iv.47 only 6 of 16 specimens dissected had developed egg rudiments (a single very small one in each of the 14 ovarioles), and in only 2 were they constricted from the germaria. By 29.iv.47 the average weight of 10 females was still only 6·3 mg. (5·5–7·0 mg.), and of these 7 had small and 3 medium fat-bodies. 6 of the females had a small egg rudiment beginning to form in each ovariole.

Ovarian development proceeds rapidly in the first half of May, and by 12.v.47 all of 10 dissected contained ripe eggs. The mean live weight had now risen to 7·3 mg. (6·0–8·0 mg.). By 22.v.47, when oviposition had not yet begun, the average weight of 6 was 10·0 mg. (9–11 mg.); the fat-body remained small to medium. The relation between increase in weight and ovarian development is indicated even in these few specimens :

Live weight (mg.)	9	10	11
Average number of ripe eggs	12	15·5	20
,, ,, of eggs + large rudiments (> ½ length of ripe eggs)	12	23	28·5

That these specimens constituted a reasonably representative sample is supported by a comparison with 220 females captured by random sweeping on 27.v.47, when the average weight was 10·4 mg.

Up to 6 eggs and egg rudiments may form in each ovariole at a time. The structural changes involved in the course of ovarian maturation are the same as described for *Notostira erratica* in Section IV (2) and as represented in figs. 5–8. The eggs during development undergo similar changes in form and assume a similar final shape. At the same time there is a lengthening of the pedicels, the formation of a small follicular plug, which is later absorbed, basal (posterior) to each egg, and the development of a larger "corpus luteum" distal to it. As in most other Heteroptera, oviposition from an ovariole is indicated by a dilated empty pedicel and the presence of a corpus luteum.

Oviposition begins in the second half of May, the time apparently depending largely on temperature conditions. In 1946, which was an "earlier" year than 1947, 5 dissected on 22.v had begun laying. In 1947 the occurrence of oviposition in dissected females was not detected until 29.v. By 10.vi.47 all of 10 dissected were laying and all had small fat-bodies. The average body weight had risen to 11·0 mg. (10–12 mg.), although the ovaries contained fewer ripe eggs than before oviposition had begun. After the commencement of egg-laying the correlation between weight and number of ripe eggs no longer strictly holds :

Date	Live weight (mg.) :—	9·0	10·0	10·5	11·0	11·5	12·0
10.vi.47	Av. no. eggs	—	6·3	10	8	6	9
17.vi.47	,, ,, ,,	13	13	—	—	15	16·3

If the effect of body size is reduced by comparing number of eggs with Wt./W.L. (W.L. = distance between apical margin of hemielytron and the proximal (inner) margin of the anal lobe), even less relation is shown :

Date.	Wt./W.L. :—	1·37	1·42–1·46	1·53	1·61	1·73	1·84	1·91
17.vi.47	Av. no. eggs	12	9	23	12	7	16·5	24

At the end of the oviposition cycle a similar absorption of egg rudiments seems to occur as in *N. erratica* (p. 180). A female captured on 25.vi.46 contained only two ripe eggs (both in one ovariole). All the other ovarioles were empty, with a total absence of egg rudiments, but with the walls crenulated, as if indicating the former position of the absorbed rudiments. The germaria were smaller than those in normal ovarioles and were yellow, resembling small apical corpora lutea. Apparently in the last stages of sexual senescence even the germaria degenerate and are resorbed.

(b) *Males.*

No sperm was present in any of the newly emerged males dissected, either in the testes or in the vesiculae seminales. The accessory glands (fig. 4) were at this time narrow and colourless and evidently not yet actively secreting. As in the females, there is, during autumn, an increase in body weight due to the deposition of a large fat-body and this is accompanied by a similar reduction in water content. Details are given in Section V. On 1.viii.47, in 2 of 5 specimens kept in captivity for nine days after emergence there were flagellate cells in the testes, but these had large heads and were not mature. The accessory glands were colourless. By 12.ix.47, although there were apparently mature spermatozoa in the testes of all field-captured specimens, none were present in the vesiculae seminales. By mid-December sperms were present in both testes and seminal vesicles and the accessory glands were white and evidently secreting. This condition was maintained throughout the rest of winter and spring. Sexual maturation is thus not completely arrested as in the females, merely apparently slowed down. Dissected females were not seen to be fertilised until early in May, so that copulation is evidently dependent on the onset of higher temperatures. It is not until this begins, with consequent rapid production and utilization of sperm, that a major drain occurs on the food reserves of the males.

(3) *Summary.*

1. *Stenodema laevigatum* (L.) is a univoltine species, both sexes of which overwinter as adults.
2. A large fat-body is laid down during autumn in both sexes. " Gonotrophic dissociation " is complete in the females, incomplete in the males.
3. The females develop no egg rudiments before or during hibernation, ovarian development being completely arrested until spring.
4. The testes and accessory glands of the males mature slowly during autumn and winter, but fertilisation does not occur until well into spring.
5. Oviposition begins during the second half of May and continues throughout June. A few eggs may be laid in July.
6. There is a rapid depletion of the fat-body in spring with the resumption of physical activity and of sexual development.
7. Few if any overwintered females survive after the end of July, while the males are reduced in numbers by the end of May and none are found by the end of June.
8. Emergence of the new generation of adults occurs during July and August.

IV. THE REPRODUCTIVE CYCLE IN *Notostira erratica* (L.).

(1) *Outline of Life-cycle.*

This grass-sucking Mirid is bivoltine, and the females only of the second (autumn) generation hibernate in the adult stage.

The eggs giving rise to the first (summer) generation of adults are laid by the overwintered females in April, May, and, as observed by Johnson (1932), in the first half of June. Most oviposition is during May. China (1925*a*) recorded the laying of two batches of 15 and 6 eggs by one female between 13–17.v.24 ; the incubation period was about 23–25 days. Johnson (1932) observed 20 instances of oviposition, in which 1–20 eggs were laid at a time. Kullenberg (1944) noted up to 16 eggs laid in a rapid series. The eggs are inserted between the leaf-blade and stem of grasses (China, 1925*a* ; Johnson, 1932 ; Kullenberg, 1942). The eggs have been described by Butler (1923), China (1925*a*), and Kullenberg (1942). Nymphs of the summer generation are found in May and June and the adults emerge during June and very early in July. First generation adults are most numerous during the first half of July, becoming reduced in numbers towards the end of this month and all dying off by, or shortly after, the middle of August. The latest capture was of two females on 16.viii.46. Sexual maturation is rapid in both sexes in the first generation and eggs are laid at the end of June and during July and early August. As seen from dissections of females and from times of the subsequent appearance of nymphs and adults, most oviposition occurs in July.

Nymphs of the second (autumn) generation occur throughout July, August and September. Adults begin to appear in small numbers towards the end of July, but the main time of emergence is in August and September. Fertilisation in this generation is in autumn, and the males then die off, none surviving the winter. The latest date for capture of males was 13.xi.47 (2). The occurrence of fertilisation is indicated in a dissected female by the dilated, yellow appearance of the bursa copulatrix, a median sac at the anterior end of the common oviduct.

It is seen from the dates given above that there are two short periods of overlap, one in early June, the other at the end of July and early August, when some adults of both generation are found together in the field. The times given all apply to southern England and, except where other reference is acknowledged, are derived from observations on field and captive specimens and from dissections.

Butler (1923) gave adult records from March to October. During the present studies both sexes have been found in November (Sunninghill, Berks., by sweeping: 4.xi.47, abundant females, fewer males; 13.xi.47, 27 females, 2 males), and hibernating females also in December (Putney Heath, London: 3.xii.46 (2)), January (Putney Common, London: 13.i.47 (33)), and February (Sunninghill: 5.ii.48 (25); 27.ii.48 (22)).

The females of the second generation overwinter at the bases of large tufts of grass. In such localities they can be found in numbers throughout winter and early spring. During cold weather they remain very sluggish and, as seen by dissection, do not feed, but become active within a few minutes of being brought to higher temperatures, when they will readily feed on green grass leaves (p. 200). Atmospheric humidity appears to be an important factor in survival of the bugs during hibernation. The bases of the large grass-tufts in which they are characteristically found are very moist without being waterlogged, the bulk and the height above ground-level of the tufts allowing quick draining away of surplus moisture. Hibernating females kept in glass tubes with moist dead grass leaves survived for 4–5 weeks, whereas those kept under dry conditions died in a few days. Butler (1923) states that in southern England the females of the second generation, which are pinkish-ochreous in autumn, assume a more or less completely green colour by late spring. China (1925*b*) notes that at Leatherhead, Surrey, the complete colour change is rarely if ever attained, only the abdomen becoming bright green, the hemielytra remaining ochreous. The overwintered females described by Johnson (1932) (May and the first half of June) also had bright green abdomens but ochreous hemielytra. Kullenberg (1944) made similar observations in Sweden, where the hemielytra, at the most, develop a narrow costal fringe of a yellowish-green colour. The present investigations give similar results in the localities mentioned in southern England. By late spring the abdomen is always bright green, but the hemielytra remain ochreous, at the most with a light greenish costal fringe and yellowish green along the veins.

(2) *Sexual Maturation.*

(a) *Females.*

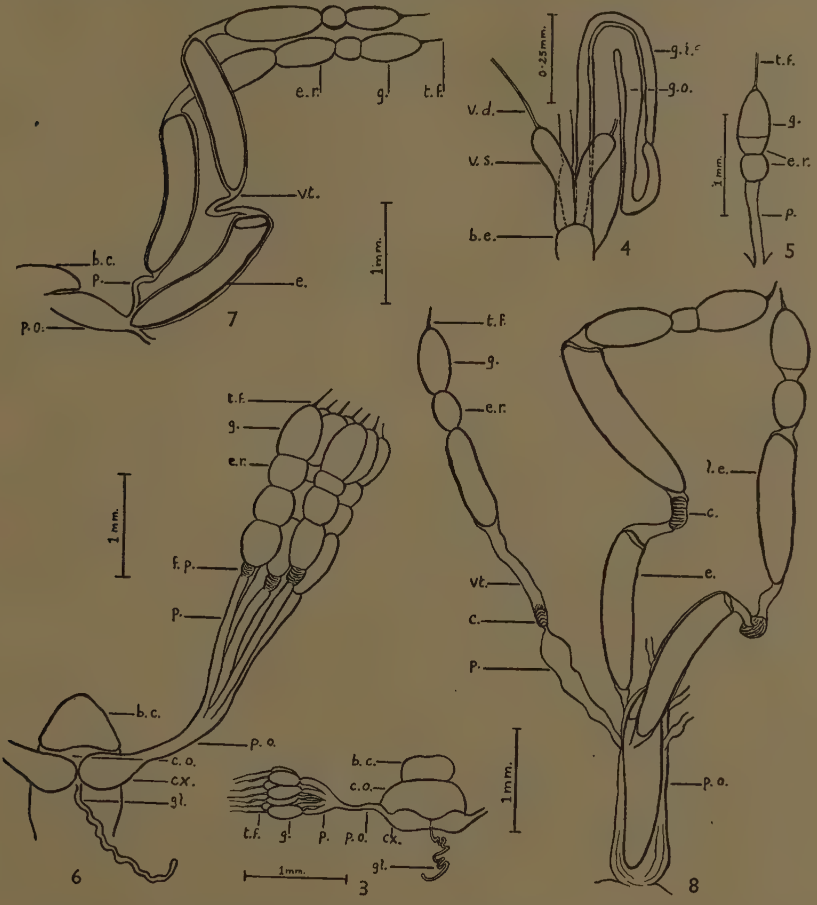
Formation of egg rudiments begins in the last (fifth) nymphal instar. Whereas in the fourth instar the ovarioles are very short, peg-like outgrowths from the apex of the lateral oviduct, with no visible separation of germaria, by the fifth instar they have considerably lengthened and each is divided into a short, tubular pedicel and an apical ovoid germarium. Before metamorphosis there is usually formed in each ovariole a single very small egg rudiment; occasionally there are two small rudiments, and sometimes none are formed until after emergence of the adults.

The sequence in ovarian development is as follows (the principal stages are shown in figs. 5–8): In a recently emerged female the paired oviducts are very short and more or less globular and the fourteen ovariole pedicels short and narrow. Each egg rudiment first appears as an opaque, whitish, more or less conical region at the base of the germarium, from which it then becomes constricted to assume a short cylindrical form, flattened at each end. The rudiments, as they separate from their neighbours and pass down the vitellarium each in its own follicle, continually increase in size and become rounded at the ends and of an elongate ovoid shape. With the formation of a chorion and the ripening of the eggs these assume their final shape, a curved cylinder with the posterior end rounded and the anterior end broader and flattened. A series of up to four egg rudiments form in each ovariole at a time. By the time two or three have formed the pedicels have lengthened, and behind the posterior end of each basal egg rudiment there is usually, though not always, a yellowish follicular plug, which however disappears as the egg ripens and passes back into the pedicel. At the distal (anterior) end of each ripening egg a white and much larger follicular plug develops, which seems to represent the last nutritional contact with the vitellarium. As the ripe egg passes further down the pedicel and finally into the lateral oviduct, the follicular plug is left behind as a "corpus luteum," now yellow in colour, at the proximal end of the vitellarium. Oviposition from an ovariole is indicated, as in most species of Heteroptera studied, by an empty dilated pedicel and a yellow corpus luteum. As the next ripe egg in turn passes back into the pedicel, the corpus luteum behind it becomes reduced in size and is eventually completely resorbed; distal to it another corpus luteum is formed in the same way. After the first oviposition the lateral oviduct is considerably lengthened and has lost its original more or less globular form.

No first generation females dissected during the first three weeks of June contained ripe eggs. Of 8 females dissected on 26.vi.47, when emergence of adults was still in progress, 5 still had short pedicels and only 1–2 egg rudiments per ovariole. In 3 others ripe eggs had developed and 2 of these had already laid, one 13 eggs, the other 14. On 11.vii.46, 2 of 3 females dissected had laid eggs (9, 14) and contained a further 13 and 5 ripe eggs respectively. By 23.vii.47, 17 of 19 females had laid eggs from all 14 ovarioles and contained an average of 16 other ripe eggs (6–22). The number of eggs ripening at one time is in agreement with the oviposition numbers observed by the writers referred to on p. 178.

Towards the end of the oviposition period the ovarioles and their contents undergo degeneration, apparently with absorption of egg rudiments. During

August, 1946, when few first generation adults remained in the field, 3 females dissected all showed signs of such degeneration. One (6.viii) contained 4 ripe eggs, 5 large and about 20 small egg rudiments. The walls of the 7 ovarioles of each ovary were more or less completely fused, and owing to this and to the indefinite outlines of the small rudiments the latter were difficult to count. These were moreover yellow, instead of the normal white colour, the changes in progress apparently paralleling those that occur in the corpora lutea, which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Figs. 3, 4.—Internal reproductive organs of *S. laevigatum*. (3) Immature ♀. (4) ♂.

Figs. 5–8.—Successive stages in ovarian development of *N. erratica*. *b.c.*, bursa copulatrix; *b.e.*, bulbus ejaculatorius; *c*, corpus luteum; *c.o.*, common oviduct; *cx*, dilated base of oviduct; *e*, ripe egg; *e.r.*, small egg rudiment; *f.p.*, follicular plug; *g*, germarium; *g.i.*, inner accessory gland (♂); *gl*, accessory gland (♀); *g.o.*, outer accessory gland (♂); *l.e.*, large egg rudiment; *p*, pedicel; *p.o.*, lateral oviduct; *t.f.*, terminal filament; *v.d.*, vas deferens; *v.s.*, vesicula seminalis; *vt*, vitellarium.

alter in colour from white to yellow and are eventually resorbed. The large egg rudiments appeared rather flattened and shrivelled. At this date, in another specimen with 4 ripe eggs the other ovariole contents seemed to have completely degenerated and no egg rudiments could be made out. In a third specimen (16.viii) no ovariole structure was apparent; the 7 ripe eggs it contained seemed to be embedded in the green connective-tissue meshwork of the exhausted fat-body.

During egg ripening there is a period of rapid increase in body weight. The average weight of 21 first generation females dissected in June and July, 1947, in which no ripe eggs had developed, was 7·0 mg. (6·5–9·5 mg.). The mean weight of 19 females in late June and July, after the formation of ripe eggs, was 11·8 mg. (9·5–14·0). The single female weighing 9·5 mg. had not yet begun laying, and it seems from the data above that this is about the critical weight for formation of ripe eggs. Wing length (W.L.) was measured as for *Stenodema laevigatum* (p. 177), and the ratio Wt./W.L. taken to eliminate as far as possible the influence of size. This ratio similarly showed an increase upon formation of ripe eggs, but there was no overlap between the two periods. In 17 females with no ripe eggs, Wt./W.L. averaged 1·31 (1·13–1·51), and in 19 females containing ripe eggs, 1·99 (1·66–2·29).

In the second generation ovarian maturation is much slower. No females dissected in autumn had more than 1–3 very small egg rudiments per ovariole. Further development is arrested by winter cold, and is quickly resumed the following year with the first onset of higher temperatures. The time of production of ripe eggs thus seems to vary from year to year according to temperature conditions. For example, in 1947 (Putney Heath, London) eggs were first observed in dissected females on 20.iii, when 2 out of 5 each contained 2 ripe eggs (= 80 per 100 females). The other females had 2 and occasionally 3 small egg rudiments in each ovariole. Green contents in the mid-gut indicated feeding by this date. By 10.iv.47, 5 of 6 females contained ripe eggs (5–22, average 15 = 1500 per 100 females) and in the other, although there were no ripe eggs remaining, oviposition had occurred from all ovarioles. In 1948 (Sunninghill, Berks.), as early as 5.ii, by which time feeding had begun, 5 females of 25 dissected had developed ripe eggs (1–14, average 5). The number of ripe eggs at the first date was 85 per 100 females and at the second date 145 per 100. By 15.iii.48, all of 3 females had ripe eggs (15–28, average 20·7, or 2607 eggs per 100 females), although oviposition had not begun. By 10.iv all 3 females dissected contained ripe eggs and 4 eggs had been laid by one of them.

The average weight of 42 second generation females before the development of ripe eggs was 8·1 mg., with Wt./W.L. 1·46. The figures for 21 females after ripe eggs had formed were 10·1 mg. and 1·76 respectively. Further details are shown by the following series:

Date.	No. ♀♀.	No. ripe eggs.		Wt. (mg.)		Wt./W.L.	
		Av.	Range.	Av.	Range.	Av.	Range.
viii.47	7	0	—	6·4	5·5– 7·0	1·16	1·02–1·39
5.ii.48	20	0	—	8·2	6·0–10·0	1·50	1·13–1·80
5.ii.48	5	5	2–5	8·3	7·0–10·0	1·59	1·32–1·79
27.ii.48	15	0	—	8·7	7·5– 9·5	1·60	1·45–1·81
27.ii.48	7	5	1–14	9·1	8·5– 9·5	1·71	1·50–1·91
15.iii.48	3	20·7	15–28	12·0	11·0–13·0	2·18	2·06–2·40

Effect of temperature on ovarian development.—Small-scale experiments on the effects of high and of low temperatures on ovarian maturation were made on the second generation females collected by sweeping at Sunninghill, Berks., on 13.xi.47, before the adults had gone into hibernation and before the occurrence

TABLE I.—*Exposure to outdoor temperatures* (*control*).

No. ♀♀.	Time dissected.	Condition of ovaries.	Size of fat-body.
2	19.xi (6 days)	14–28 very small egg rudiments	Medium.
7	9.xii (26 days)	20–42 ,, ,, ,, ,,	,,
		At both dates, pedicels short; no follicular plugs	

Ovarian development in all nine was normal for females taken in the field at this time.

TABLE II.—*Exposure to* — 4° *C.*

Time at —4° C.	Condition of ovaries.	Size of fat-body.
3½ days	(i) (Dead) No distinguishable rudiments	Medium.
	(ii) ,, 14 very small rudiments	,,
19 ,,	(i) 28 ,, ,, ,,	,,
	(ii) ,, ,, ,, ,,	Large.

At both dates, pedicels short; no plugs

TABLE III.—*Exposure to —4° C. followed by 25° C.*

Time at —4° C.	Time at 25° C.	Condition of ovaries.	Size of fat-body.
3½ days	2 days	26 small egg rudiments. Pedicels short, with no follicular plugs	Medium.
,, ,,	19 ,,	34 rudiments, the basal ones up to 4 × length of others. Pedicels longer, with a very small follicular plug proximal to each basal rudiment	Small.
5½ ,,	15 ,,	(i) (Dead) 2 ripe eggs, 2 large and 24 small rudiments. Pedicels elongate, with larger plugs	Exhausted.
,, ,,	,, ,,	(ii) 29 rudiments, as in 2nd case above. Pedicels elongate, with small follicular plugs	Small.

TABLE IV.—*Exposure to 25° C.*

Time at 25° C.	Condition of ovaries.	Size of fat-body.
3½ days	(i) 28 small egg rudiments	Medium.
,, ,,	(ii) 14 ,, ,, ,,	,,
	Pedicels short in both, with no plugs	
8 ,,	(i) 42 small egg rudiments	Small.
,, ,,	(ii) 28 ,, ,, ,,	,,
,, ,,	(iii) 25 ,, ,, ,,	,,
	Pedicels longer in all, with small follicular plugs	
15 ,,	(i) 9 ripe eggs, 2 large and 21 small rudiments	,,
,, ,,	(ii) 2 ,, ,, 2 ,, ,, 26 ,, ,,	,,
	Pedicels elongate in both, with large plugs	
20 ,,	3 ripe eggs, 4 large and 35 small rudiments	,,
	Pedicels elongate with large plugs	

Egg rudiments > ½ length of ripe eggs are described as large.

of any frost. The insects were kept in cylindrical cages 15 in. high and 8 in. in diameter, with transparent celluloid sides and the lid perforated for aeration. For food, young barley seedlings were planted in a flower-pot of soil in each cage; the soil was kept moist and the plants kept lightly sprinkled with water. The barley was renewed at the first signs of deterioration. Those bugs subjected to a temperature of — 4° C. were kept with grass in muslin-capped tubes and left in a refrigerator.

Conclusions.—It is seen that ripe eggs can be formed within 15 days of exposure to 25° C. and that preliminary exposure of females to low temperature (around F.P.) is unnecessary for ovarian maturation. If anything, subjection to a temperature as low as —4° C. indeed appears rather to have an inhibiting effect on subsequent development. In these experiments ripe eggs had been formed by the end of November and the beginning of December, some three or four months before their production at outdoor temperatures in the field.

The results even of these small experiments indicate that there is no obligatory diapause in the ovarian maturation of overwintering females of *N. erratica*, but that egg development, begun in autumn, is simply arrested by low temperatures during winter, production of ripe eggs proceeding with the resumption of warmer weather in spring. In this respect the species differs from the allied grass-feeding Mirid *Stenodema laevigatum*, which, throughout autumn and winter, undergoes a complete diapause in ovarian development, the breaking of which would seem to necessitate the previous operation of factors additional to high temperature. The question is further discussed in Section V.

(b) *Males.*

The males of the second generation, unlike the females, suffer no arrest of sexual development but, as in the first generation, mature quickly, fertilising the females in autumn and dying before winter. There is no ripe sperm in the testes of newly emerged males, and their vesiculae seminales are translucent and narrow and the accessory glands colourless. Second generation males dissected on 2.ix.47, after being kept on grass plants in a cage until 9 days after emergence had ripe sperm in the testes but not in the vesiculae seminales and there were abundant white secretions in the basal half of the accessory glands. First generation males taken in the field (Sunninghill) showed some white contents in the accessory glands for the first time on 26.vi.47 and by then the testes contained ripe sperm. By 22.vii.47 all of 10 males dissected had ripe sperm in both testes and seminal vesicles, the latter being dilated and of an opaque white appearance, and the accessory glands were full of white granular secretions. The presence of sperm in the vesicles and of secretions in the glands appears to indicate a physiological stage of readiness for copulation. These male secretions possibly help to nourish the sperm during its retention in the bursa copulatrix of the female; such nutrition would be particularly necessary in the hibernating generation, in which the sperm is retained in the female throughout winter before fertilization of eggs ensues.

(3) *The Two Generations of* N. erratica.

(a) *Introduction: Historical.*

Gulde (1921), working on German material, was apparently the first to demonstrate that *N. erratica* has two egg-laying generations per year, a green summer generation and an ochreous autumn generation, the females of the latter overwintering. Kullenberg (1944) similarly recorded two generations in southern and central Sweden. There appears to be no previous record of the bivoltinism of this species in Britain. The present investigations have demonstrated the existence of two generations of this bug, at least in southern England, the first, with a comparatively short adult life and rapid sexual maturation, emerging in early summer, the second, in which the females overwinter and begin oviposition in spring, emerging during late summer and early autumn.

A form of *N. erratica*, pinkish above and light green below, had been described by Costa (1852) as a distinct species, *Miris tricostatus*. Fieber (1860–61) described two colour varieties of the adult, a green one, *virescens*, occurring during the summer, and a reddish or yellowish-brown form, *ochracea*, found in autumn, but gave no indication of the relations between them. In 1911 Reuter raised Fieber's var. *ochracea* to the status of a species, *Notostira ochracea*, and shortly after (1912), having discovered Costa's earlier description, maintained that this species was the same as *M. tricostatus* Costa, which thus became *N. tricostata* (Costa). Gulde (1921) considered *N. tricostata* to correspond to the brown autumn generation of *N. erratica*.

Butler (1923) noted that the green summer females are larger than the ochreous females found in autumn, and moreover that the former have proportionately longer antennae. He pointed out that the situation cannot be so simple as in *Stenodema*, in which there is a similar difference in colour between autumn and spring (overwintered) females, since there can be no increase in size of individual adults during winter. He quoted Reuter (1911) as inclining to the belief that the two forms of *Notostira* represent two distinct species, but pointed out that " there are not the same differences in the males ; structurally these are all alike and they differ only in depth of coloration. . . . In Oshanin's *Katalog* (1912), *ochracea* Fieb. is given as a distinct species under the name of *tricostata* Costa. In that case we have the curious phenomenon of two species with entirely different females, but with identical males."

China (1925*b*) has described the rearing, in captivity, of a green adult from an egg laid by an ochreous, overwintered female, thus demonstrating conclusively that the two colour forms are of one and the same species.

(b) *Size Differences between the Two Generations.*

Saunders (1897) pointed out that the female of the brown form of *Notostira* has shorter legs than the green form, and Butler (1923) described, as indicated above, the greater size of the green females and their proportionately longer antennae and legs.

In the present study the adults of the two generations have been compared statistically for wing-length (as a criterion of size), length of the second antennal segment (L.2A.S.), and the ratio between these two measurements (W.L./L.2A.S.). Wing-length (W.L.) was measured with an ocular micrometer, and was taken as the distance between the distal apex of the hemielytron and the proximal (inner) margin of the anal lobe when the hemielytron was kept between a slide and coverslip. All three values were found to be overlapping in range for the two generations, but, in the females, distinctly bimodal, with the means significantly different. The frequency distribution curves of these values are given in figs. 9 to 14. In Table V are given the ranges of the three values and the means with their standard deviations and coefficients of variation.

TABLE V.—*W.L., L.2A.S., and W.L./L.2A.S. in the two generations of* Notostira erratica.

	W.L.				L.2A.S.				W. L./L.2A.S.			
	Range (mm.).	x (mm.).	σ.	V.	Range (mm.).	x (mm.).	σ.	V.	Range	x.	σ.	V.
♀♀:												
Gen. I.	5·52–6·51	5·88	0·21	3·57	2·77–3·47	3·20	0·14	4·38	1·68–2·07	1·84	0·08	4·35
Gen. II.	4·88–6·20	5·50	0·26	4·73	2·42–3·03	2·68	0·13	4·85	1·83–2·40	2·05	0·11	5·37
♂♂:												
Gen. I.	5·34–6·13	5·69	0·19	3·34	3–06–3·63	3·30	0·15	4·55	1·54–1·98	1·73	0·07	4·05
Gen. II.	5·08–5·91	5·56	0·20	3·60	2·84–3·54	3·28	0·16	4·88	1·58–1·81	1·69	0·07	4·14

The means of W.L. and L.2A.S. are significantly greater in the first (summer) than in the second (autumn) generation of females, while the ratio W.L./L.2A.S. is significantly lower (i.e., proportionate as well as absolute antennal length is greater in the first generation).

♀♀: W.L. . . . $n = 136$, $t = 9{\cdot}0303$, $p < 0{\cdot}001$.
L.2A.S. . $n \doteq 143$, $t = 7{\cdot}0469$, $p < 0{\cdot}001$.
W.L./L.2A.S. $n = 136$, $t = 12{\cdot}0519$, $p < 0{\cdot}001$.

Since presumably the average genetic constitution is essentially similar in the two generations, it would appear that environmental conditions during nymphal life are responsible for the greater size of the females of the first generation. It is conceivable that some of the factors involved are nutritional, since probably the nutritive value of the grass sap is different in spring, when the nymphs of the first generation are developing, and in late summer and early autumn, the feeding period for second generation nymphs. From experiments of Davidson (1923) on the growth and reproduction of *Aphis rumicis* on bean plants, "it appears that the cell-sap of the young growing tissue of the host-plant is of a very definitely higher nutritive value . . . than the older tissues."

It was at first thought that the proportionately greater antennal length in the larger females of generation I might be accounted for by a simple process of heterogonic (allometric) growth, representable by a single curve taking in both generations, and with the ratio W.L./L.2A.S. decreasing uniformly with increase in W.L. But in fact, as shown in fig. 15, heterogony must proceed in the reverse direction to this, and at a different rate in the two generations. With greater W.L., W.L./L.2A.S. *increases*, i.e., proportionate antennal length decreases. But in generation I the former ratio rises less steeply than in generation II, with the result that proportionate antennal length always remains greater. These results suggest certain hypotheses, some of which might be tested experimentally. Assuming one or more growth activators to which wing length and antennal length are differentially responsive, it would seem that their action is influenced by the different environmental conditions (nutritional, temperature, etc.) holding in the two generations, so as to effect a divergence in the rate of heterogony.

It would now seem likely that, in both generations in England, two different genetic populations occur, comprising two varieties (see p. 190), and the implications of this dimorphism require further consideration. Judging, however, from Kullenberg's results (1944), both varieties are not necessarily to be found together in any one locality; in Sweden they were found to have different geographical distributions, apparently only occasionally overlapping. The frequency distribution curves (figs. 9–14) for the wing and antennal lengths of the English specimens used in the present study indicate either that only one form, differing in these measurements, is involved, or that, if the two varieties are present, one occurs in such small numbers as to have no significant effect on the conclusions reached. Subsequent examination of material from the localities worked on (including the hemielytra of females and the male genitalia) has revealed only one form, apparently referable to Kullenberg's variety II, the more widespread variety in Sweden.

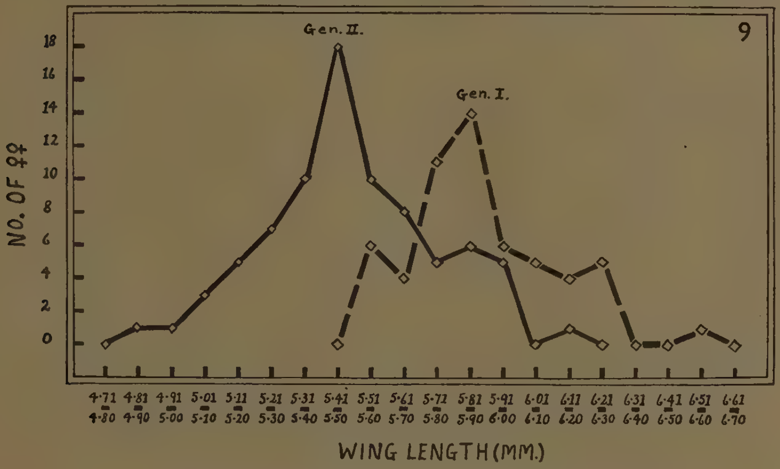


FIG. 9.—Frequency distribution curves for wing length in the females of the two generations of *N. erratica* (L.).

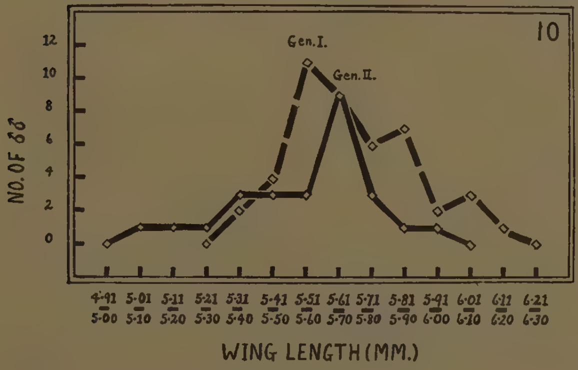
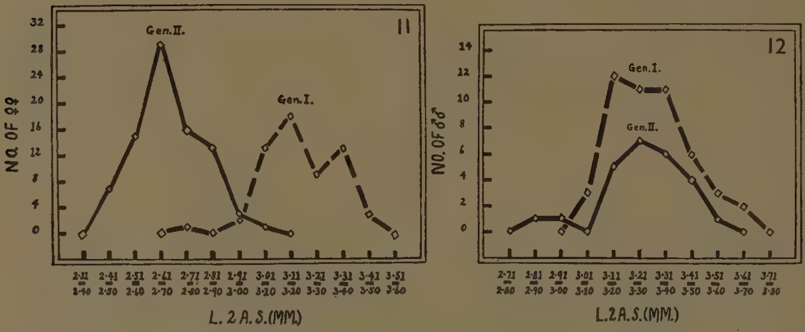


FIG. 10.—Frequency distribution curves for wing length in the males of two generations of *N. erratica* (L.).

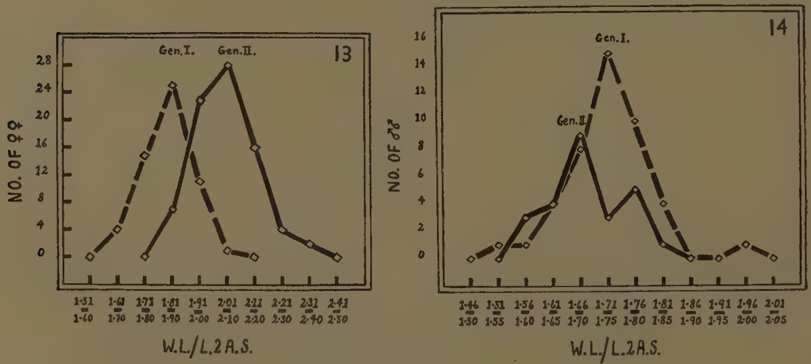
In the males, the mean W.L. in the first generation is also significantly greater than in the second, although the difference is not so great in this sex. L.2A.S. is, on the other hand, not significantly different in the two generations.

In both generations, antennal length, both absolute and relative, is considerably greater in the males than in the females, and this is perhaps to be correlated with the greater activity of the males in searching for mates.

♂♂ : W.L. . . $n = 71$, $t = 2{\cdot}7332$, $p < 0{\cdot}01$.
L.2A.S. . $n = 73$, $t = 0{\cdot}5259$, $p > 0{\cdot}50$.
W.L./L.2A.S. $n = 69$, $t = 2{\cdot}2730$, $p < 0{\cdot}05$.



Figs. 11, 12.—Frequency distribution curves for L.2A.S. in the two generations of *N. erratica* (L.). (11) Females. (12) Males.



Figs. 13, 14.—Frequency distribution curves for W.L./L.2A.S. in the two generations of *N. erratica* (L.). (13) Females. (14) Males.

While the mean W.L. of the first generation males is 2·3 per cent. greater than in second generation males, the corresponding increase in the first generation females is 6·6 per cent. For antennal length, the difference between the two generations of males is negligible (0·6 per cent.), but the average for the first generation females is 19·4 per cent. greater than in the second. With W.L./L.2A.S. there is a small difference in the males (a 2·4 per cent. increase in Gen. I) and, in the females, an increase of 11·4 per cent. in Gen. II.

As seen from Table V, in both sexes all three values are more scattered relative to the mean in the first generation than in the second. It may be that the first generation of bugs is subjected to a more variable range of conditions during the critical stages of development than is the second. The difference between the coefficients of variation of the means in the two generations is in each instance greater in the females than in the males. A comparison with *Stenodema laevigatum* shows that the W.L. of *Notostira*, at least in the females, is somewhat more variable than in the former species. The coefficient of

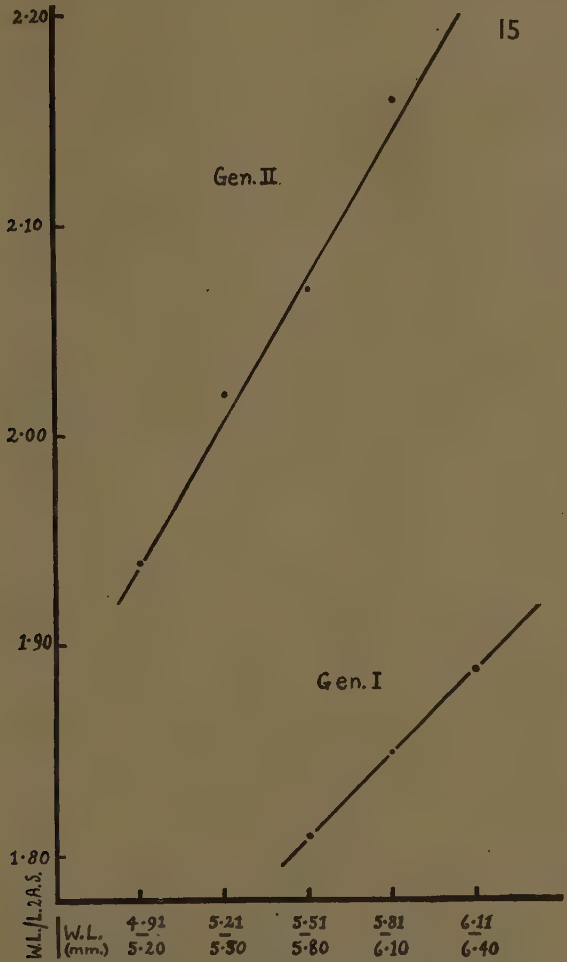


Fig. 15.—Relation between W.L. and W.L./L.2A.S. in the females of the two generations of *N. erratica* (L.).

variation in females of *Stenodema* is 3·40 against 4·73 in females of the second generation of *Notostira* and 3·57 in the first (average of 4·15); in males of *Stenodema*, 3·45 against 3·60 in the males of the second generation and 3·34 in the first (average of 3·47).

The differences between the females of the two generations of *N. erratica* may be summarised thus:

(1) The females of the first, non-hibernating generation have a much shorter adult life than those of the second, which hibernate.

(2) The maturation period of second generation females is much the longer, ovarian development being interrupted by the low temperature conditions of winter.

(3) The males of both generations being similar in their rate of sexual maturation, there is a much longer interval between fertilisation and oviposition in the second generation.

(4) While there is no appreciable accumulation of fat reserves in the females of the first generation, in those of the second there is a pronounced increase in the size of the fat-body before hibernation.

(5) Both body size (estimated by wing length) and proportionate antennal length are significantly greater in the females of the first generation.

(6) Whereas the females of the second generation are ochreous, with (in the present studies) never more than a faint trace of green found in the hemielytra even in overwintered specimens, the first generation females are always entirely green.

(c) *Two Varieties of* N. erratica.

Kullenberg (1944) has recorded from Sweden two morphologically different varieties in this species, each of which has two generations a year. Unfortunately his work was not encountered until after completion of the present studies, which, however, as pointed out above, apparently involved only one of these forms.

Variety I of Kullenberg is characterised by its smaller size (particularly in the females of the overwintering generation), by the convex outer margins of the hemielytra of the females and in the males by a shorter left clasper with a wider apex (1944: Taf. 4). Variety II has a larger size, almost parallel-sided hemielytra, and a longer left clasper in the males, with a narrow apex. The two varieties are similar in colour. Their distribution within Sweden is different, that of variety II being the more extensive. Kullenberg does not consider the two forms sufficiently distinct to rank as different species, and indeed, particularly in the females, has found considerable intergradation between the extremes.

In England, Butler (1924) had described five forms of females in *N. erratica* and four forms of males, distinguished by morphological and colour differences. Kullenberg considers that the female 1 and female 2 of Butler probably correspond to the summer generation of his variety II, female 3 to the same generation of variety I, and female 4 and female 5 to the autumn generation of varieties I and II respectively. Butler's male 4 he regards as probably equivalent to variety I and the remaining three forms of males to variety II. According to Butler (1924), Hutchinson found two different shapes to the left clasper of the males of *Notostira* in England, but there seems to be no further record of the differences involved. From these findings of Butler and Hutchinson it appears that the two varieties of Kullenberg do occur in England; further study is desirable to determine their relative distribution, both numerical and geographic, in this country.

(4) *Summary.*

1. *N. erratica* (L.) is bivoltine in southern England, with a summer and an autumn generation of adults.
2. Sexual maturation is rapid in the first generation, but in the second only the males mature by autumn, dying after fertilising the females. The latter overwinter in a sexually immature condition, and do not develop ripe eggs until the following spring.
3. The arrest in ovarian development is shown to be caused by the low temperatures of winter and its resumption to depend on exposure of the females to higher temperatures. There is no obligatory diapause such as seems to occur in *Stenodema laevigatum*.
4. The morphological changes involved in ovarian maturation are described. At the end of the oviposition period there appears to be a resorption of egg rudiments.
5. Both body size (estimated by wing length) and proportionate antennal length are significantly greater in first generation females than in those of the second generation. In the males body size is also greater in the first generation, although the difference is much less than with the females. Attention is drawn to the probable occurrence in England of two varieties of *N. erratica*, both bivoltine and differing in size and in the form of the left clasper of the male, as described by Kullenberg in Sweden.
6. The adults of the second generation are ochreous, the overwintered females undergoing little or no colour change; those of the first generation are green.

V. CHANGES IN THE FAT, SOLIDS, AND WATER CONTENTS IN *S. laevigatum* AND *N. erratica*, AND THEIR RELATION TO THE REPRODUCTIVE CYCLE.

(1) *Technique.*

Size of fat-body was estimated by two methods:

(i) Visual estimation based on dissection of individual specimens. Fat-body was classified rather arbitrarily into three size-groups described respectively as "small," "medium," and "large." Experience in the dissection of large numbers of bugs gives a basis for reasonably consistent grouping.

(ii) Determination of the average fat content of specimens collected in the field by random sweeping. For this purpose, "total fats" were extracted with technical (ethyl) ether (S.G. 0·720) in a Soxhlet from ground, water-free material (oven-dried at 110° C. to a constant weight), and the resultant extract dried to constant weight in a desiccator.

The same material was used to estimate percentage of water and of total solids. Owing to the small size of the bugs, individual estimations were impracticable with this technique, but a picture of the average constitution at different times of the year was obtained by using fairly large numbers of insects in each instance. (The numbers are given in the tables.) To prevent desiccation, specimens were kept during collection in previously weighed air-tight containers.

Although much smaller accumulations of fat occur in other parts of the body the main mass of adipose tissues is found in the abdominal cavity, and it is this to which the term "fat-body," as understood in the following accounts of dissections, is applied. The fat-body, as in other Heteroptera, comprises a series of lobules, invested in a connective-tissue network, arranged in parietal layers around the abdominal cavity and extending to a greater or less degree among the viscera and, in its maximum development, largely filling the spaces between them. There is not, however, as in some insects, any definite visceral layer closely enveloping the gut.

(2) *Fat-body Size: Visual Estimation.*

(a) *Stenodema laevigatum* (L.).

At the beginning of the season 1947–48, in early July, when emergence had just begun, all adults dissected had small fat-bodies. Although definite lobules were present, they contained little fat, and the number of lobules obvious on dissection was comparatively small. Towards the end of this month the average size of the fat-body had already increased considerably. On 24.vii.47, when emergence was still in progress, the possible range in adult age of field-collected specimens was from less than one day to about three weeks. All adults had at this time a greater or less number of obvious lobules, from which a film of fat arose on dissection, but the number of such lobules varied considerably in different specimens, probably in the main according to length of time since emergence. The fat-bodies of 17 females dissected at this date were classified as 4 small, 10 medium, and 3 large. Of 6 males, 4 had small fat-bodies and 2 large. In early August (by which time emergence of new adults had ceased) the fat-bodies of all bugs dissected were medium to large. By the latter half of August almost all had large fat-bodies, and this condition was maintained in the majority of specimens throughout autumn and winter, apparently owing to the greatly reduced activity of the bugs during the colder months. A reduction in size of the fat-body became evident only in the early part of April, when the development of egg-rudiments had begun, for which process and for the spring renewal of activity generally the food reserves are evidently heavily drawn upon. A similar depletion in the males is no doubt to be attributed during the latter part of winter to the demands of sexual maturation and, in May, to those of copulation, which involves production and expenditure of sperm and considerable physical activity, the males flying actively during the period of mating in search of the females. Further, according to Kullenberg (1944) the males appear to have stopped feeding by this time. The production of ripe eggs, which appeared in the first half of May, and oviposition, beginning during the latter part of this month, is a further considerable drain on these reserves in the females. By that time the fat-bodies of all adults dissected were small or only medium. During the period of renewed feeding beginning in spring no further accumulation of fat reserves appears to occur, all the food material obtained from the plant hosts being used to supplement the reserves in supplying the demands of the greatly increased activities of the insects. When the food reserves are used up, the amount of nutriment obtained by feeding is apparently insufficient to maintain egg production (see also p. 205). The production and laying of eggs continues throughout June, and the fat-bodies of all specimens dissected during this month were small to very small. By the end of June the lobules had been entirely or mainly exhausted of their contents (with little or no film arising on dissection), leaving visible only the connective-tissue network, which is stained deep green by the pigments of the body fluid.

Colour of fat-body and blood.—In approximately half of the nymphs and the newly emerged adults of both sexes the fat-body appears, on dissection, of a more or less pronounced greenish colour, and in the others colourless and translucent. The green colour, however, is of a superficial nature, and due to the presence of green pigments in the body fluid of the abdominal haemocoele. It is soon removed by the water during dissection, whereupon the formerly " green " fat-body assumes the appearance of the unpigmented type. " Fat-body colour " is always indicated by the external colouring of the ventral surface of the abdomen, which is either green or pale to brownish cream, according to whether the fat-body is " green " or colourless. Owing to the translucence of the abdominal sternites, even the intensity of the green pigment of the blood is reflected in the shade of green presented by the abdomen. There is, before hibernation, no increase in the proportion of bugs with " green " fat-bodies, nor is there at any time during this period any significant difference either in size (W.L.) or in body weight between bugs with " green " fat-bodies and those in which the fat-body is colourless. Evidently there is no increase in green pigmentation with age during autumn, and throughout this season the insects seem to retain the abdominal colouring obtaining at emergence. In pigment-containing nymphs the dorsal surface of the abdomen is also green, but this is always black in the adults, the colour of the blood being masked by the dark pigment of the tergites.

In spring the fat-body assumes a deep green appearance in all specimens, and the ventral surface of the abdomen in the females becomes an intense grass-green. Early in May the hemielytra of the females also begin to take on a green colour, at first mainly along the costal margin. By the middle of this month the females are completely green except for the black abdominal tergites and the tarsi, the apices of the tibiae and the two apical and distal half of the third segments of the antennae, which remain reddish-brown. The males do not show this colour change except on the ventral surface of the abdomen, which usually becomes greyish-green, and on the legs and basal antennal segment, which are often greenish-brown. The change to a green colour is apparently due to the accumulation in the blood of pigments, perhaps derived from the plant food in too great a quantity to be entirely excreted (green granules appear in the Malpighian tubes), their presence being first apparent, externally, in the abdomen, but later, with an increased concentration, becoming evident also in the hemielytra and appendages. The males become more darkly pigmented in spring, and the colour effect of the green blood is thus largely masked.

(b) *Notostira erratica* (L.).

There appears to be no notable accumulation of food reserves in the females of the first generation. The rapid maturation of the ovaries apparently utilises nutriment as fast as it is assimilated from the plant hosts. Of ten last instar nymphs, nine had small fat-bodies and one a medium sized fat-body. During June and July, 1947, the proportion of small to medium fat-bodies in adult females was 18 : 3. By August, when adults were greatly reduced in numbers and the oviposition cycle was at its close, with the degeneration and apparent resorption of egg rudiments noted above (p. 180), the fat-body was completely exhausted, no lobules being observed and no film of fat rising on dissection.

The females of the second generation, on the other hand, do accumulate fat reserves before going into hibernation, though not to the same extent as in *Stenodema laevigatum*. A comparative account of this process in the two species, based on the results of Soxhlet extractions, is given below. Dissection gives a similar picture. Nymphs and also adult females captured in July and early August all had small fat-bodies. The fat-bodies of females dissected in autumn and the first half of winter were medium to large, while of females dissected during February, when the formation of ripe eggs was beginning, 7 had small, 34 medium, and 6 large fat-bodies. By April the fat-body was usually small. The fat-body is usually coloured more or less green by pigments in the blood, and is invariably of a very deep shade of green in late winter and spring. As in *Stenodema laevigatum*, the colouring is superficial, and on dissection in water is soon removed from the lobules. These are then revealed as colourless and translucent in autumn ; the fat-body of overwintered females, however, has undergone a change in colour, being yellow when the green pigment is removed.

There is no appreciable cycle of fat-body size in the males of either generation. Those of the second generation, being much shorter lived than the females, and not overwintering, have no need of an accumulation of food reserves in the autumn. In both generations the fat-body of the males remains small to medium throughout life.

(3) *Extraction Methods.*

In Tables VI and VIII are set out the changes in constitution (fat, water, and solids content) of males and females of *S. laevigatum* and of the second (overwintering) generation of *N. erratica* between the beginning of the pre-hibernation feeding period and its close.

(a) *Fat Content.*

As already indicated, dissection reveals a rapid increase in size of fat-body in *S. laevigatum* during the period of active feeding that follows emergence in mid-summer. This increase, accompanied by a progressive increase in body weight, was seen to continue until about the beginning of September, when the fat-bodies of almost all specimens dissected could be referred to the " large " category. Soxhlet extraction of fat confirms that the fat content of these insects reaches a maximum at about this time.

The average fat content in recently emerged females (range of adult age between 3 weeks and less than 1 day), collected on 25.vii by random sweeping in the field, was 25 per cent. dry weight or 8 per cent. of live weight. The average live weight at this time was 6.4 mg. By 5.ix the mean body weight had increased to 7.3 mg. and the fat content to 48 per cent. of dry weight (25.5 per cent. of live weight). At the same time there was a marked decrease in water content, from 67 per cent. of body weight in the earlier collections to 47 per cent. in the later. Thus, with a rise of 14 per cent. in the average body weight coincident with an increase of dry weight from 33 to 53 per cent. of live weight, there had been, during this period, a considerable accumulation of solids, the greatest part of which was made up of fat. Non-fatty solids increased only from 25 per cent. of live weight (74·4 per cent. of dry weight) to 27 per cent. of live weight (52 per cent. of dry weight). A comparison of the weights of the several constituents in an average female at the two dates is revealing. Despite the increase in body weight there was a loss of 20 per cent. of the original water, while against this the solids content increased by 82·5 per cent., the amount of fat by 258 per cent. and of non-fatty solids by 25·6 per cent. Comparable changes take place in the males, which were closely similar in constitution to the females at both dates (Table VI).

By the middle of June, towards the end of the oviposition period, when the fat-bodies of all bugs dissected were classified as small or very small, the average fat content in the females (15.vi.47) was reduced to the very low figure of 14 per cent. of dry weight. The average live weight at this time was 10·9 mg., this high figure being due to the presence of ripe eggs. The actual fat reserves of the females must have been even smaller than the percentage figure indicates, since this includes also the fatty substances in the eggs. It is seen from Table VII that the water content had increased to the normal (non-hibernating) condition.

In the second generation of *N. erratica* there is also a building up of fat reserves in the prehibernation feeding period, accompanied by an increase in live weight (Table VIII). This period is, however, notably shorter than in *Stenodema*, since emergence is a month later. As is seen from Table IX, the amount of fat stored up is, in both sexes, considerably smaller than in *S. laevigatum.* This difference may be due in part to the difference in length of the feeding period in the two species, but it is perhaps to be related more particularly to the more favourable environmental conditions enjoyed by *Stenodema*, because of its earlier emergence. The adults of *Stenodema* are able to feed during mid- and late summer, when the average temperature is higher and the nutritive value of the plant sap possibly greater than during the autumn months to which the second generation adults of *Notostira* are in the main restricted. That these differences may influence the building up of the fat-body even in the nymphal stages is suggested by the fact that the percentage of fat in the females of *Notostira* is about the same towards the end of the prehibernation feeding period as near the beginning of this period in *Stenodema* females.

Although shortly after emergence the two sexes in each species contain a similar percentage of fat (much smaller in *Notostira* than in *Stenodema*), a notable difference appears between the two species in the relative ability of the two sexes to lay down further fat (Tables VI and IX). Whereas in *Stenodema* the percentage of fat in the males by the end of the feeding period reaches essentially the same value as in the females, in *Notostira* the proportion of fat in the males is only 63 per cent. that in the females.

Table VI.—*Changes in constitution of* S. laevigatum *between* 25.vii.47 *and* 5.ix.47 (*in the period between emergence and hibernation*).

	Av. wt. (mg.).				%Increase or Decrease in Wt. between 25.vii and 5.ix.		Wts. as % of Current Live Wt.			
	♀♀.		♂♂.		♀♀.	♂♂.	♀♀.		♂♂.	
No. bugs .	87	37	95	33						
Date (1947) .	25.vii	5.ix	25.vii	5.ix			25.vii	5.ix	25.vii	5.ix
Live wt. .	6·40	7·30	5·10	5·60	+ 14	+ 9·8	100	100	100	100
Wt. water .	4·28	3·43	3·36	2·80	− 20	− 16·7	67	47	65·8	50
Dry wt. .	2·12	3·87	1·74	2·80	+ 82·5	+ 61	33	53	34	50
Wt. fat .	0·52	1·86	0·49	1·34	+258	+175	8	25·5	9·5	24
Wt. non-fatty solids	1·60	2·01	1·25	1·46	+ 25·6	+ 16·5	25	27·5	24·6	26
Wt. fat as % of Dry wt.							24·6	48	28	48
Wt. non-fatty solids as % of Dry wt.							75·4	52	72	52
Increase in Wt. fat as % of increase in Dry wt.							76·6		80·5	

Table VII.—*A comparison of constitution of females of* S. laevigatum *near beginning and near end of adult life.*

	Av. weight.		% Increase in Wt. between 25.vii and 15.vi.	Wts. as % of Current Live Wt.	
	25.vii.47 (mg.).	15.vi.47 (mg.).		25.vii.	15.vi.
Live wt.	6·40	10·90	70	100	100
Wt. water	4·28	7·15	67	67	65·6
Dry wt.	2·12	3·75	77	33	34·4
Wt. fat	0·52	0·525	1	8	4·8
Wt. non-fatty solids	1·60	3·225	102	25	29·6
Wt. fat as % of Dry wt.				24·6	14
Wt. non-fatty solids as % of Dry wt.				75·4	86

Table VIII.—N. erratica : *Second generation : Comparison of constitution at beginning of adult life and at pre-hibernation stage.*

	A. wt. (mg.).				% Increase or Decrease in Wt. between 5.ix and 1.xi		Wts. as % of Current Live Wt.			
	♀♀.		♂♂.		♀♀.	♂♂.	♀♀.		♂♂.	
No. bugs	218	205	142	28						
Date (1947)	5.ix	1.xi	5.ix	1.xi			5.ix	1.xi	5.ix	1.xi
Live wt.	6·80	8·00	5·00	5·30	+ 18	+ 6	100	100	100	100
Wt. water	4·90	4·80	3·50	3·60	− 2	+ 3	72	60	70	68
Dry wt.	1·90	3·20	1·50	1·70	+ 68	+ 13	28	40	30	32
Wt. fat	0·15	0·71	0·15	0·30	+373	+100	2·2	9	3	5·7
Wt. non-fatty solids	1·75	2·49	1·35	1·40	+ 42	+ 4	25·8	31	27	26·3
Wt. fat as % of Dry wt.							8	21·5	10	17·8
Wt. non-fatty solids as % of Dry wt.							92	78·5	90	82·2
Increase in Wt. fat as % of increase in Dry wt.							43		75	

Table IX.—*Change in fat content of adult from beginning to end of pre-hibernation period.*

Sex.	% Increase in Wt. fat.		Time.	Wt. of fat as % of Live wt.		Wt. of fat as % of Dry wt.	
	Stenodema laevigatum.	*Notostira erratica.*		*Stenodema laevigatum.*	*Notostira erratica.*	*Stenodema laevigatum.*	*Notostira erratica.*
♀	285	373	Beginning of period	8	2.2	24·6	8
			End of period	25·5	9	48	21·5
♂	175	100	Beginning of period	9·5	3	28	10
			End of period	24	5·7	48	17·5

	Average increase in weight of fat.		Average weight of fat at end of period.	
	S. laevigatum.	*N. erratica.*	*S. laevigatum.*	*N. erratica.*
♀	1·35 mg.	0·56 mg.	1·86 mg.	0·71 mg.
♂	0·85 mg.	0·15 mg.	1·34 mg.	0·30 mg.

Discussion on fat cycle and reproductive cycle.—Kullenberg (1944) has noted that, unlike the females, the males of *S. laevigatum* in Sweden appear not to feed or to feed very little during the autumn and, in view of the similarity of fat content in the two sexes of this species in autumn, this would seem a further indication of the importance of the earlier phases of the feeding period. A difference in feeding habits between the two species, observed by Kullenberg in Sweden, may also relate to the disparity in fat storage. According to this writer, while *S. laevigatum* sucks mainly the young seed-heads of grasses, *N.*

erratica shows a decided preference for the leaves and leaf-sheaths. It is in the seeds and their embryos that one might expect a higher concentration of food-substances, and in particular the oily constituents and vitamin B.

Apart from these differences in nutritional and other environmental factors, which may well provide an important and immediate basis for the different rate of fat storage in the two species, there are other and more general considerations bearing on the process. These concern important differences in the reproductive cycle itself. Firstly, whereas in the second generation of *Notostira* copulation is in the autumn and the males die with the onset of colder weather, none surviving the winter, in *Stenodema*, males as well as females hibernate, and fertilisation takes place the following spring. Thus, while in males of the latter species there is a delay in sexual maturation and activity, involving a degree of " gonotrophic dissociation," with the development of a large fat-body, in *Notostira* the fat-body remains small and the males become sexually active in a relatively very short time after emergence. It is, doubtless, valid to regard the amount of fat laid down as in causative relation to the length of adult life; the males of *Notostira*, having in autumn utilised food supplies in the production and expenditure of sperm and in the activities of mating, lack the reserves which in *Stenodema* enable the males successfully to withstand winter conditions.

But besides this immediate physiological sequence in the individual, the presence or absence of a large fat-body may also be considered from the long-range view-point of species evolution. It seems probable that, given a genetic tendency for either autumn or spring fertilisation, selection would favour the establishment of " gonotrophic dissociation " in the latter case and its absence in the former. A compromise might well be wasteful, as leading to reduced sperm production and sexual activity in the autumn without providing an adequate food reserve to ensure successful hibernation. The selective value of both early sexual activity and lack of fat deposition might well be enhanced in the males of a bivoltine species such as *Notostira*, by its necessarily having, in the second generation, a period of adult feeding of comparatively short duration under unfavourable conditions. The genetic and environmental factors supposed to be involved would, in such circumstances, be mutually reinforcing.

Outstanding differences appear also in the nature of the reproductive cycle in the females of the two species. From experiments described above (pp. 183-4) it is seen that ovarian development in the overwintering generation of *N. erratica* involves no true or " obligatory " diapause, but is dependent on the maintenance of sufficiently high temperatures. In both generations of *Notostira* the first distinguishable egg rudiment in each ovariole is separated off from the germarium at so early a stage as the last (fifth) nymphal instar. In the adult, further development leading to the production of ripe eggs proceeds rapidly and without interruption in the first generation, while, in the second, up to three small egg rudiments are formed in each ovariole by autumn or early winter, subsequent development being arrested by cold and its resumption depending on exposure to higher temperatures, the exact time at which this occurs varying from year to year. The arrest in development is of a " facultative " type, and can be prevented entirely by subjecting the females to high temperatures without the necessity for any previous exposure to low temperatures (i.e., around F.P.).

In the univoltine *S. laevigatum*, on the other hand, there are never distinguishable egg rudiments at emergence and, despite the long period of high temperatures to which the females are subjected during mid- and late summer, none are formed until spring. In other words, *Stenodema* undergoes an "obligatory" diapause of some sort in ovarian development.

The exact nature of this diapause remains to be elucidated. The facts described above suggest two possible factors in the breaking of diapause and as prerequisites for ovarian maturation: these are fertilisation and a previous period of exposure to low temperatures. The writer has unfortunately had to leave England before testing these factors. It is highly desirable that temperature experiments, similar to those made on females of *Notostira*, should be carried out on both females and males of *Stenodema*. The possible influence of fertilisation on ovarian development should also be determined. The effect of cold in breaking diapause is a very general one which has been noted by many workers in a wide range of insect species and at various stages in the life-cycle (Wigglesworth, 1942: 9, 69). It is known that fertilization is of varying importance in inducing egg formation in different species of Heteroptera, being necessary for the production of mature eggs in the bed-bug, *Cimex lectularius* L. (Cragg, 1923), whereas virgin females of the Triatomid *Rhodnius prolixus* Stål will develop and lay infertile eggs (Buxton, 1930). The evidence already presented (Sect. III (2)), indicates that in *S. laevigatum* egg rudiments may begin to form in early spring before fertilisation of the female occurs. It is possible, then, that fertilisation is not necessary for the initiation of oocyte formation, though it may be a prerequisite for "maturation." This would seem to point to a preliminary exposure to cold as a factor in the initial breaking of reproductive diapause in this species. In *N. erratica* the lack of dependence of the early stages of oocyte formation on fertilsiation is obvious, since the development of egg rudiments has already begun at the time of emergence. In this species, also, it still remains to be demonstrated experimentally whether fertilisation is necessary for the complete growth of eggs and oviposition.

It is necessary to keep in mind the two main stages of oocyte development in the telotrophic type of ovariole found in the Heteroptera, the first dependent on nutrition by the nurse cells of the germarium, and the second on follicular nutrition by the cell walls of the vitellarium. It is likely that different factors are involved at these two stages. Wigglesworth (1936, 1948) has shown that a secretion of the corpus allatum is necessary for the production of ripe eggs in the Triatomid bug *Rhodnius prolixus*; without it the egg rudiments die and are absorbed at the stage when their nutrition is taken over from the nurse cells by the follicular cells. Weed (1936) (Mrs. Pfeiffer (1939, 1945)) has similarly shown that a corpus allatum hormone functions in the production of "ripe" eggs in the panoistic grasshopper *Melanoplus*, and concludes that its effect is a nutritional one concerned with the utilisation of fatty materials. While nothing is known of the functions of the corpora allata in the Miridae, from the similarity of action and the non-specificity between different species and families that Wigglesworth (1936) has demonstrated for the moulting and nymphal hormones in the Triatomidae and Cimicidae, it seems not unlikely that the sequence of hormone action will prove to be similar on other Heteropteran families also. If this be so, the factors involved in the early stages of oocyte formation in *Stenodema* would have to be related to initiation of mitosis and to nurse cell nutrition, and those concerned in "ripening" of eggs to hormone control of the utilisation and transference of nutritive materials by the follicular cells. The latter relation might be either direct, by stimulation of the corpora allata at some critical period, or indirect, by influencing the brain or other centre controlling the sequence of activity of the corpus allatum (*vide* Wigglesworth, 1948), or by bringing about physiological changes in the reproductive system which make it responsive to the action of the maturation hormone. On the other hand, the factors discussed above might prove to be concerned solely with the initiation of oogenesis, i.e., with the breaking of reproductive diapause in the strict sense. In any case, in a complete study of this problem the stages in egg formation must be clearly differentiated.

Another question that might be investigated is whether the absorption of egg rudiments at the end of the reproductive period, which has been observed in *N. erratica* and *S. laevigatum*, is due to senescence of the corpus allatum and reduction of its secretion, or to nutritional or other general physiological causes. Perhaps both might apply at different stages in egg development. The eventual degeneration of the germaria which apparently occurs in *Stenodema* (p. 177) would be an immediate cause of death and resorption of the younger oocytes. Joly (1942 ; 1945), after demonstrating the function of the corpora allata in egg maturation and oviposition in the Dytiscidae, attempts to reconcile the apparently different results of corpora allata extirpation in different insects and postulates concurrent processes of growth and degeneration ; in insects in which the nutritive cells show prolonged activity or in which ovarian development is rapid the latter may be completed even in the absence of a maturation hormone, whereas in those with a more prolonged reproductive cycle the degenerative processes may have time to take effect after a certain period if the insects are deprived of corpora allata.

Whether the requirement for ovarian maturation in *Stenodema* should prove to be one or other of the two factors discussed above, or a combination of both, the condition of diapause undergone is obviously a firmly established phase of the reproductive cycle, a rigid adaptation to winter conditions. The result is the establishment of a strictly univoltine cycle which insures against the development of immature stages during unfavourable times of the year. It stands in contrast to the much more labile and " opportunist " cycle of *Notostira*. The differences between the two species suggest the possibility of climatically different centres of origin or a difference in the time of establishment in colder regions (Dr. O. W. Richards, *personal communication*). However, at the present time both species are widely distributed in the Palaearctic region.

The results of these investigations accord with the views of Dr. W. E. China, of the British Museum (expressed verbally), on the relative evolutionary status of the two species. *N. erratica* he regards as a variable species at present in a condition of active evolutionary development and in process of splitting up into forms which will eventually become adapted to different environments and which may be regarded as incipient species. The genus *Stenodema*, on the other hand, has already become divided into several comparatively stable species adapted to particular environments. The comparative instability of *N. erratica* is seen both structurally, in its tendency to split into varieties, apparently with different geographical ranges, and in the greater variability, particularly in the females, of such measurements as wing length and antennal length, and also physiologically, in its lack of the rigidly determined reproductive cycle and " gonotrophic dissociation " found in *S. laevigatum*. The bivoltinism of *Notostira* may be regarded as one aspect of its " opportunist " life-cycle, reproductive development proceeding whenever and so long as temperature conditions permit. Kurdjumov (1913) has stated that in South and Central

Russia *N. erratica* hibernates in the egg stage; if this is so it provides a further example of the relative plasticity of the reproductive cycle in this species. Such instances of plasticity, together with the fact that *Notostira*, although variable, comprises but a single species, lends further support to the possibility suggested above that this genus has had a more recent origin and dispersal than *Stenodema*, which comprises several species and is represented in the Nearctic as well as in the Palaearctic region.

To sum up the relations between fat-body cycle and reproductive cycle in the two species under consideration, there is to be seen a series in the degree of "gonotrophic dissociation" involved. In the males of *N. erratica* there is no appreciable laying down of fat-body and the attainment of sexual maturity and activity is a rapid process. The females of the second generation of the same species show incomplete "gonotrophic dissociation," developing before winter a fat reserve greater than that achieved by the males but considerably smaller than that in either sex of *Stenodema*, and the ovaries can develop at any time given a sufficiently high temperature. In both sexes of *Stenodema laevigatum* a large fat-body is laid down; in the males, although some sperm is produced by winter, there is no sexual activity and no appreciable drain on food reserves until the spring; in the females, "gonotrophic dissociation" is complete and egg rudiments fail to develop before winter, although the adults are subjected to temperature and nutritional conditions apparently much more favourable than those sufficient to initiate ovarian development in *Notostira*.

In hibernation a distinction is to be drawn between physical activity of the insect and suppression of mitotic activity and growth generally, as involved, e.g., in gonad development. Neither *Notostira* nor *Stenodema* are completely inactive except at very low temperatures, and both can be induced to walk, although rather sluggishly, when disturbed during cold weather in their winter quarters. Moreover, the hibernating females of *Notostira* and both females and males of *Stenodema* resume normal locomotory activity within a few minutes after being brought into warm surroundings, and the males, the more active sex, will in such circumstances readily fly. When thus reactivated, the females at least will almost immediately begin to feed if provided with fresh young shoots of grass.

(b) *Water Content.*

The two species are also markedly different in the extent of water loss before hibernation and, as with fat storage, while the sexes of *S. laevigatum* are similar in respect of water content, the males and females of *N. erratica* show appreciable differences. In *Stenodema* the water content of the females drops from 67 per cent. of live weight near the beginning of the feeding period to 47 per cent. towards its close, and, in the males, from 66 to 50 per cent. In *Notostira* second generation females there is also an appreciable, though smaller water loss, the percentage decreasing from 72 to 60 per cent. The males, however, show no such significant loss, the water content being 70 per cent. at the earlier date and still 68 per cent. at the later. The actual decrease in the weight of water in an average individual is strikingly different in the two species (Table X). In the female there is a loss of 0·85 mg. (20 per cent.) in *Stenodema* and of only 0·10 mg. (2 per cent.) in *Notostira*. In the male of *Stenodema* the decrease is 0·56 mg. (16·7 per cent.), while in the male of *Notostira* there is, despite the slight decrease in percentage of water, actually a small gain in the weight of water of 0·10 mg. (3 per cent.).

This difference between the sexes in *Notostira* may be put down to the requirements of hibernation, which apply to the females but not to the males. Evidence of the effects of supercooling, associated with water loss, in promoting cold hardiness in hibernating insects, has been put forward by a number of writers, e.g., Cousin (1932) in the larvae of the blow-fly *Lucilia*, Bodine (1923) in the nymphs of the grasshopper *Chortophaga*, and Payne (1927 ; 1928) in the beetle *Popillia.*

The difference in the extent of water loss between females of *Stenodema* and of *Notostira* may be partly related to the fact that ovarian diapause is more complete in the former species than in the latter. In *Notostira*, which is able at any time to take advantage of favourable temperature conditions to further ovarian development, there is perhaps a compromise between the retention of a water content sufficiently high to facilitate such a process and its reduction to a point which will confer adequate cold hardiness. But this is a problem requiring further experiment, for Salt (1936) has shown that in some species of insects, including the bugs *Leptocoris* (Coreidae) and *Chlorochroa* (Pentatomidae), loss of water has no effect on supercooling. Moreover, Payne (1927) has demonstrated that the water content and the amount of water lost during the season at which cold hardiness is developed vary considerably in different species of insects.

Fink (1925), working on the potato beetle *Leptinotarsa decemlineata* Say, found during the period between active feeding and hibernation a loss in the percentage of water content and a gain in the percentage of fat content closely approximating to the results obtained here for *S. laevigatum*, particularly in the female. In *Leptinotarsa* the water loss is by 20 per cent. (76·4 to 56 per cent.), and the gain in fat by a little more (7·8 to 29 per cent.). In the females of *Stenodema* the water content decreases by 20 per cent. and the fat content rises by 17·5 per cent., while for the males the corresponding figures are 15·8 and 14·5 per cent. The values for these two species stand in marked contrast to the results obtained for *Notostira* : a loss in water content by 12 per cent. in the females and by 2 per cent. in the males, and a gain in fat by 6·8 per cent. in the females and 2·7 per cent. in the males. But Fink pointed out that in *Leptinotarsa* the diminished water content appears to have no effect in increasing cold hardiness, at all events at temperatures below F.P., for this species in hibernating always burrows in the ground to a depth of 10 to 18 inches, presumably as a protection against extremes of cold, and if experimentally a covering of only several inches is allowed during winter there is a mortality of 100 per cent. There is no such peculiarity of behaviour in *Notostira* to distinguish it from *Stenodema*

TABLE X.—*Water content : changes from beginning to end of pre-hibernation feeding period.*

Sex.	% Decrease or Increase in Wt.		Time.	Wt. Water as % of Live Weight.		Actual Decrease or Increase in Wt. Water in average Individual.	
	S. laevigatum.	*N. erratica.*		*S. laevigatum.*	*N. erratica.*	*S. laevigatum.*	*N. erratica.*
♀	−20	−2	Beginning of period	67	72	−0·85 mg.	−0·10 mg.
			End of period	47	60		
♂	−16·7	+3	Beginning of period	65·8	70	−0·56 mg.	+0·10 mg.
			End of period	50	68		

during hibernation, but factors other than water loss may play roles of different importance in relation to cold hardiness in the two species. For indeed it appears that, in general, degree of cold hardiness is not dependent on any one factor. Kozhantshikov (1938), for example, in discussing the relation of cellular respiration to cold hardiness after dehydration, shows that the quality of the fats present is probably of greater importance than the quantity. This is a consideration to be held in mind also in the matter of the difference in fat storage between the females of the two species.

(c) *Non-fatty Solids.*

The data for changes in weight and percentage weight of non-fatty solids during this feeding period in average specimens of *S. laevigatum* and *N. erratica* are summarised in Table XI. From these figures it is seen that, during this period of increase in body weight, the females of both species and the male of *Stenodema* show an appreciable increase in these constituents, both absolutely and as a percentage of live weight; in the male of *Notostira* this latter percentage is slightly decreased. The decrease in the proportion when expressed as a percentage of dry weight is of course due in all cases to the greater accumulation of fats. The difference in the actual increase in weight of non-fatty solids between the male and the female of *Stenodema* is seen to be largely due to the greater increase in body weight in the latter; the proportion of these substances at both the beginning and the end of the period is very similar in both sexes.

A large proportion of the non-fatty solids may probably be taken as proteins, and the similarity of the two sexes in laying down these substances in *Stenodema* and the discrepancy between them in *Notostira*, after allowing for difference in body weight, may well be related to the dissimilarity in sexual behaviour already noted. Unlike the males of *Stenodema*, those of *Notostira* have, before winter, already completed copulation, and have thus drawn heavily on the protein substances which enter so largely into the constitution of the sperm.

TABLE XI.—*Non-fatty solids: changes from beginning to end of pre-hibernation feeding period.*

Sex.	%Increase in Wt.		Time.	Wt. as % of Live Wt.		Wt. as % of Dry Wt.	
	S. laevigatum.	*N. erratica.*		*S. laevigatum.*	*N. erratica.*	*S. laevigatum.*	*N. erratica.*
♀	25·6	42	Beginning of period	25	25·8	75·4	92
			End of period	27·5	31	52	78·5
♂	16·5	4	Beginning of period	24·6	27	72	90
			End of period	26	26·3	52	82·2

(4) *Summary.*

1. In *N. erratica* (L.) there is no appreciable storage of food reserves in the first generation, nutriment being rapidly utilised in sexual maturation. In the females of the second generation, however, there is a notable increase in fat and total solid contents in the feeding period before hibernation, drawn on mainly for egg production in the following spring. Corresponding autumnal increases are much less in the non-hibernating males.

2. There is also, in this species, a decrease in percentage water content of the females before hibernation. No such decrease occurs in the males during the same period.

3. Both increase in fat content and decrease in water content are considerably smaller in the females of *N. erratica* than in either sex of *S. laevigatum.* The sex and species differences in these respects are considered in relation to the requirements of hibernation and the cycle of sexual development in the two species.

4. In the females of *S. laevigatum* there is complete "gonotrophic dissociation," with an obligatory diapause in ovarian development intervening as a rigid adaptation to winter conditions. The males of this species resemble the females in degree of fat storage and of water loss. Although some sperm are produced by winter, copulation never occurs until spring, and there is no great drain on food reserves until then.

5. In the males of *Notostira* there is no arrest of sexual development and no "gonotrophic dissociation." In the females the arrest is facultative and "gonotrophic dissociation" incomplete; the formation of egg rudiments begins early, but maturation is delayed by the low temperature of winter.

6. The possible significance of the differences in the reproductive cycle of *Notostira* and *Stenodema* is discussed. The factors involved in breaking the reproductive diapause in *Stenodema* and in ovarian maturation are considered (particularly low temperature and fertilisation), and suggestions made for further desirable lines of research.

VI. THE REPRODUCTIVE CYCLE IN *Myrmus miriformis* (FALLÉN).

(1) *Introduction: Habitat and Feeding.*

This species, a Coreid of the subfamily Rhopalinae (Corizinae), is an inhabitant of "grass-heath" or *Agrostis-Festuca* communities, and in the present study (at Sunninghill, near Ascot, Berks.) was found to be severely restricted to such areas in which shallow-rooting grasses like *Agrostis canina* L., *Festuca ovina* L., *F. myuros* L., *Holcus mollis* L., *Deschampsia flexuosa* (L.), and *Sieglingia* (*Triodia*) *decumbens* (L.) Bernh. predominated, mixed with "calcifuges" such as *Rumex acetosella* L. (sheep's sorrel), *Calluna vulgaris* (L.) Hull and *Erica cinerea* L.

In its flattened, sub-parallel form and the green colour which predominates among the females, it departs rather sharply from the typical Coreid facies and converges in general appearance towards that of many grass-frequenting Mirids. In particular, the form and general brachyptery of *Myrmus* females parallel closely the condition met with in *Leptopterna.* The females are usually considerably larger than the males. The live weight of 16 males captured during July ranged between 4·0 mg. and 8·5 mg. (average 5·5 mg.). During the same period, when emergence and oviposition were simultaneously in progress, the weight of 16 females ranged between 7·0 mg. and 17·5 mg. (average 11 mg.).

So far as has been observed, this species is entirely phytophagous. While it has been seen to feed on grass leaves, there seems to be a definite preference for the unripe seeds of grasses. Both in the field and in captivity it was observed sucking the seeds of various species of grasses, and both nymphs and adults kept in cages concentrate on the seed-heads for feeding. In this respect *Myrmus* resembles the grass-sucking Mirids *Stenodema laevigatum* (p. 174) and *Leptopterna dolabrata* L. (Butler, 1923; 373).

(2) *Dimorphism.*

M. miriformis displays alary dimorphism in both sexes. Any specimen may be readily classified as either brachypterous or macropterous. Although there is considerable variation in the wing-length of brachypterous forms, there is a pronounced difference in development between even the longest winged of such bugs and the macropterous forms, in which alone the hemielytra cover the tip of the abdomen. The brachypterous type is by far the commoner (95 per cent. of those collected). Of 80 males captured in the field by random sweeping during the summer of 1947, 77 (96 per cent.) were brachypterous. Of 135 females similarly obtained, 127 (94 per cent.) were brachypterous.

The males are dimorphic also as regards colour. 59 (77 per cent.) of these brachypterous males were brown and only 18 (23 per cent.) green. All three of the macropterous males were brown, but the numbers caught do not preclude the possibility of the occasional occurrence of green macropterous males. On the other hand, all the females captured, both brachypterous and macropterous, were green.

(3) *Reproductive Cycle.*

The species is univoltine and overwinters only as an egg, which is the stage of longest duration in the life-history, lasting for 8–10 months. Hatching occurs during May and emergence of adults mainly in July but extending into August, while a few adults were captured in the field during the last week of June, 1947.

(a) *Fertilisation.*

Sexual maturation is rapid and copulation takes place throughout the months of July, August and September. Both sexes mate many times during life. From dissection and observations of copulation in the field and in captivity it is seen that the females are fertilised both before ripe eggs are produced and subsequently at frequent intervals during the oviposition period. Pairs are still seen *in copula* towards the end of September, when egg-laying is drawing to a close. Since the formation of egg rudiments begins in the fifth instar nymphs, evidently fertilisation is not necessary for the initiation of ovarian development, though it may be a prerequisite for maturation and oviposition.

This species copulates very readily ; pairing frequently occurs in tubes and cages almost immediately after capture. The copulatory position is end-to-end, the larger female dragging the male with her when she moves and often feeding while *in cop.* The act of copulation is usually of long duration, lasting for several hours. Pairs have been observed continuously *in copula* for periods of 4 to 10 hours, and others remained paired, at least during the daylight hours, over a period as long as 24 hours. The sperm is stored in the single spermatheca of the female, an ovoid receptacle opening by a slender duct into the middorsal surface of the vagina, in which fertilisation takes place as the eggs pass through it just before oviposition.

(b) *Ovarian Development.*

There are seven ovarioles to each ovary. Formation of recognisable egg rudiments has already begun in the last (fifth) nymphal instar, in which a single small oocyte is separated off from the germarium in each ovariole. Comparatively few egg rudiments are present in the adult at any given time. In each ovariole the basal egg always " ripens " (i.e., develops a tough chorion) and is laid while the more distal egg rudiments are still very small. Thus there is never at any time more than one " ripe " egg, with chorion and micropylar processes developed, in each ovariole, and there is always a very great disparity in size and form between such an egg and the more apical rudiments. Of the latter, there are usually two, sometimes only one, per ovariole.

Up to two or three ripe eggs usually accumulate in each lateral oviduct before being laid. The eggs when laid are usually brown, though not infrequently they are almost white or of a pale greenish shade, and, on the other hand, eggs still within the female, particularly those situated most basally in the lateral oviducts, have often already attained a brown colour. The extent of darkening of the chorion at the time of oviposition may thus depend largely on the length of time the eggs have been retained within the female. A larger proportion than normal of dark brown eggs has been noted in the oviducts of females kept under laboratory conditions, which often seem to delay oviposition of eggs ready to be laid.

(c) *Oviposition.*

Oviposition occurs throughout the months of July, August and September. Dissection indicates that the eggs must be laid in batches of no more than 14–20 at a time, with distinct intervals between batches. This is seen to be so in practice, batches of about 12 eggs being normal at the height of the oviposition period, laid, firmly attached to grass or heath leaves and stems, either singly or closely side by side in a single line. Owing to the fact that the several ovarioles become to a greater or less extent " out of step " in the production of ripe eggs, and that from one to three eggs may accumulate in each lateral oviduct before being laid, the number of eggs laid at a time varies. Up to 19 eggs have been recorded from one female during a single period of egg-laying activity. Towards the end of life, owing perhaps partly to depletion of reserve foods and the deterioration in nutritive value of available plant food, egg production slows down and the number of eggs laid drops considerably, to as few as one at a time.

It proved extremely difficult in the laboratory to provide the conditions necessary for a normal life-span and for normal egg-production and oviposition. Dissection showed that females often died either without producing ripe eggs or having failed to lay such eggs stored up in the ovarioles and lateral oviducts. Thus a reliable figure for the total production of eggs per female could not be obtained.

The base of each ovariole pedicel becomes dilated after an egg has left it for the lateral oviduct, and the presence of such empty and dilated tubes is an indication that oviposition has probably begun or at least is shortly about to begin. When empty, dilated pedicels occur in a female the lateral oviducts of which are devoid of eggs, or in which there are fewer oviducal eggs than dilated pedicels, it is certain that oviposition has already commenced. There is no noticeable formation of corpora lutea in this species.

(4) *Fat-body.*

The fat-body is well developed at emergence and, indeed, in the fifth instar nymphs. In both nymphs and adults the fat-body is superficially coloured green owing to the presence of green pigment in the blood. As with similar pigments in other species of phytophagous Heteroptera investigated, it is readily removed from dissected specimens by soaking or washing with water. In this, as in other species, it would seem to be a by-product of nutrition, derived eventually from the plant food. Besides white excretory substances, a green pigment is often found within the Malpighian tubes.

There is a progressive depletion of the fat reserves after emergence, to supply the needs of rapid sexual maturation and of oviposition, so that, towards the end of the oviposition period, the fat-body has become greatly reduced. Most of the fat-lobules have been exhausted, leaving little but the connective-tissue framework. The short-lived adult of *Myrmus* thus presents quite a different type of fat-body cycle from that passed through in bugs such as *Stenodema laevigatum*, in which the adult overwinters before becoming sexually mature.

(5) *The Egg.*

(a) *Description.*

The egg of *M. miriformis* is invested in a tough chorion, usually of a shining brown colour. Averaging 1·2 mm. in length and 0·3 mm. in greatest width, it is of a curious form, roughly oval, but with each side flattened by a broad depression. A pair of thickened longitudinal ridges, bounding the ventral margin of the lateral depressions, sharply demarcate the ventral edge of the egg. The dorsal surface is not marked off from the sides in this way and is wider than the ventral. The egg when laid thus presents four principal surfaces: the two sides, similar and concave, and the convex dorsal and ventral edges, the former broader than the latter. If the egg is soaked in water it eventually swells up, the lateral depressions rounding out to make the sides convex, and the egg assumes a more nearly oval appearance. The dorsal edge then presents a continuously curved surface with the sides, but the ventral surface is still clearly marked off by its lateral ridges.

There are several regions of the egg in which the chorion displays certain obvious modifications of structure. The ventral edge of the egg, owing to the curvature of the marginal ridges, appears in full view as of an elongate dumb-bell shape. The wide anterior third of this surface is comprised by the operculum, a chorionic plate pyriform in outline (widest anteriorly) and sloping obliquely ventrad from the posterior pole of the egg. The operculum is further marked off from the rest of the egg-shell by a narrow margin of lighter colour, representing the future line of dehiscence at hatching. The operculum is completely or almost completely separated from the rest of the shell by the emerging nymph, breaking away cleanly along the suture line. The external surface of the operculum is covered by a series of minute, flattened papillae, giving it a finely granular appearance.

Situated medially, at the anterior end of the egg, is a pair of small, comma-shaped chorionic (micropylar) processes, two stalk-like outgrowths 0·12 mm. in length, with their free ends incurved in frond-wise fashion. Their apices are much more darkly pigmented than the rest. One of the processes is set on the operculum itself, a short distance back from its anterior margin; the other originates from the smooth, dorsal chorionic surface at an approximately equal distance on the other side of this margin. One process is thus slightly ventral, the other slightly dorsal to the anterior pole of the egg.

Arising from a slight depression in the centre of the dorsal surface is a very short black stalk, its outer end expanded as a flattened disc, by which, at oviposition, the egg is attached to a plant leaf or stem by means of a secretion of the female. So firm is the attachment that on removing the egg a strip of plant epidermis usually comes away with it, and occasionally the stalk itself breaks off.

When the egg is laid, its anterior end (with the micropylar processes) is always directed upwards, the ventral surface being outermost from the substratum, and the opercular area, through which the young nymph escapes at emergence, facing upwards and outwards. The egg is figured by Butler (1923 : pl. III, f. 1).

(b) *Water Relations of the Egg.*

As shown by experiments detailed below, *Myrmus* eggs when laid contain sufficient water for complete embryonic development and emergence of the nymph, and so are independent of any external supply. Excessive soaking in water, indeed, inhibits development and, if prolonged, eventually has a lethal effect. Under normal conditions it must be very difficult for any appreciable amount of water to enter the egg. The whole surface of the chorion is markedly hydrofuge and impermeable and, as shown below, the only points at which water could enter are through the two small micropyles at the apices of the chorionic processes. The impermeability of the shell would also prevent excessive loss of water from the egg throughout the long period of hibernation. So far, then, as water is concerned, the egg of *Myrmus* appears under normal conditions to form an essentially closed system during diapause and development.

Effects of aqueous solutions on the chorion.—Observations were made on the reactions of the egg to various aqueous solutions (stains and solutions of NaOCl). Ingress of such solutions was, in the intact egg, restricted entirely to the two micropyles. Owing to the extremely hydrophobe nature of the entire shell surface the eggs are very resistant to wetting, and to submerge them for treatment with reagents it was necessary to weigh them down with filter-paper.

In the course of attempts to remove the chorion using Slifer's (1945) method, eggs were immersed in aqueous solutions of NaOCl ranging from 3 to 10 per cent. In all of 50 eggs so treated, the micropylar processes and an area of chorion around their bases was affected. The first noticeable result was a thinning and depigmentation of the areas involved, and this was first evident around the bases of the two processes as a pale disc which, with continued treatment, increased in extent peripherally. Eventually the chorion in this region was completely dissolved and a jagged hole produced in the shell. At the same time the micropylar processes themselves were gradually dissolved away. Except when the chorion was elsewhere damaged, as described below, this anterior region was the only part of the shell to be affected until a later and general stage of chorion disintegration. Evidently the solution entered the egg through the micropyles and accumulated inside the shell at the base of the processes, from which centre it gradually diffused, at the same time dissolving the chorion from within. Thus it is apparent that the whole surface of the egg-shell is impermeable to water, which can enter only through two small apertures, the micropyles themselves. The restriction of this ingress to the micropylar region is nicely emphasised by the way in which the pale, thinning disc of chorion intersects the opercular area (on which one only of the two processes is situated). Further, although the chorion of the opercular suture is obviously thinner and weaker than elsewhere, this relative thinness has no apparent effect on its permeability. The impermeable region is presumably an external waxy layer such as has been described on the eggs of many insects and other Arthropods.

From some eggs the dorsal stalk had become detached, and in all these a second circular area of pale, thin chorion, and eventually a hole, developed mid-dorsally, coincidentally with the anterior area. This never occurred in eggs with intact stalks, so that it would appear that in removing the stalk the more permeable inner layers of the chorion were exposed. These facts indicate that the stalk is not involved in any absorption of water from the plant tissues to which it is so firmly attached. Moreover, eggs removed from the leaves on which they were laid and subsequently kept dry, and those laid on dead leaves (a common oviposition site, both in the field and in captivity, when both green and dried leaves are available), remain alive and eventually hatch. In this respect their reaction contrasts with that of similarly attached sawfly eggs as recorded so early as 1740 by Réaumur, who found that these eggs soon collapsed and died when the willow leaves on which they were laid were allowed to dry. When allowed to develop normally, the sawfly eggs doubled their original volume, owing to absorption of water from the plant tissues. A similar example is described by Weber (1931) in the egg of the Aleyrodid *Trialeyrodes vaporariorum* Westwood, which absorbs water through an attachment stalk from the leaf on which it is laid, and which shrivels and dries if the leaf dries out.

Myrmus eggs fixed and stained with acid fuchsin or with Mallory's triple stain show staining reactions in precisely similar areas to those affected by solutions of NaOCl; that is, a disc around the base of the micropylar processes is stained, as are, less deeply, the processes themselves. Here, again, the evidence is for entry of the stain through the micropyles, its accumulation inside the base of the processes, presumably in a respiratory gas pocket, and its gradual diffusion in the adjacent tissues within the egg. The mid-ventral region stains only when the attachment stalk has been removed.

In view of the extremely small size of the apertures and the strongly hydrofuge nature of the adjacent chorion, it seems very doubtful that any appreciable amount of water should in fact normally enter the egg in the field, and this is certainly unnecessary. At the tips of the micropylar processes of eggs kept experimentally on a moist substratum small bubbles are frequently to be seen, an indication of the normal function of the micropyles in the respiratory exchange of gases.

Discussion.—In their independence of an additional supply of water from the environment, the eggs of *M. miriformis* differ from those of the sawfly and the Aleyrodid mentioned above and of many other species of insects which when laid do not contain sufficient water for complete development. A review of the indirect evidence for such requirement of an external source of water by insect eggs is given by Uvarov (1931), Needham (1931) and Buxton (1932). In the Acrididae, Bodine (1929), Roonwal (1936), and Birch and Andrewartha (1942), working on *Melanoplus differentialis* Thomas, *Locusta migratoria* (L.), and *Austroicetes cruciata* Saussure respectively, showed that the increase in weight of the developing egg is due to an increasing water content, and Slifer (1938) demonstrated the necessity for absorbed water in the development of the eggs of *M. differentialis* and Salt (1949) in *M. bivittatus* (Say).

There appears to be little experimental evidence for the water requirements of the eggs of Heteropteran species. Such evidence is given by Johnson (1934, 1937) for the Mirid, *Notostira erratica*, by Banks (1949) for *Corixa punctata* Illiger (Corixidae), and by Beament (1949) for the Triatomid, *Rhodnius prolixus* Stål, the eggs of all of which absorb water during development. These, unlike the eggs of *Myrmus*, are laid in an aqueous or moist medium. The observations of Altson (1933) show that the eggs of *Dysdercus* (Pyrrhocoridae), which are laid in the soil, need moisture for their development, and similar requirements no doubt apply to the eggs of large numbers of Heteroptera laid in wet or moist surroundings.

(c) *Diapause and Development of the Egg.*

The eggs laid in July, August and September do not hatch until the following May. Thus for a period of 8–10 months during autumn, winter and spring the embryo remains in a condition of arrested development. That this arrest, at least in the great majority of eggs, is in the nature of an obligatory diapause not

TABLE XII.—*Development and hatching of eggs of* M. miriformis *under experimental conditions.*

Exp.	Treatment.	No. Eggs used.	Eggs developing.		Eggs hatched.	
			No.	%.	No.	%.
1	Constant temperature of 25° C.	175	12	6·7	4*	2·3
2	Outdoor t°, followed by C.T. of 25° C.					
a	7–14 days at outdoor t°; to 25° C. in late autumn (19 and 26.xi.47)	20	0	0	0	0
b	35–47 days at outdoor t°; to 25° C. in early winter (17 and 31.xii.47)	20	7	35	1	5
3	Exposed to winter lab. temps. Transferred to C.T. of 25° C. on 31.i.48					
a	Kept dry at 25° C.	25	15	60	7	28
b	Kept moist at 25° C.	25	13	52	0	0
4	At − 8° C. for 3½–27 days; then to C.T. of 25° C.	80	6	7·5	2	2·5
5	At − 4° C.; then to C.T. of 25° C.					
a	7 days at − 4° C.	10	7	70	1	10
b	15 days at − 4° C.	10	7	70	5	50
c	21 days at − 4° C.	10	6	60	3	30
d	35 days at − 4° C.	10	6	60	2	20
e	Totals	40	26	65	11	27·5
6	Xylol treated					
a	Then kept moist at C.T. of 25° C.	50	13	26	0	0
b	Then kept dry at outdoor temps.	24	22	91·7	21	87·5
7	Kept at outdoor temperatures					
a	Dry	110	106	96·4	51	46·4
b	Moist	45	43	95·6	26	57·8
c	Totals	155	149	96·1	77	49·7

* Only 2 hatched successfully. In one the operculum was partly dehisced but the embryo was dead inside. In another the head only emerged, the nymph dying in this position.

Table XIII.—*Development and hatching of eggs of* M. miriformis *at outdoor temperatures.*

Date.	Total No. Eggs at Stage:				Total Developing.
	(1.)	(2.)	(3.)	(4) (hatched).	
7(*a*) 110 eggs kept dry:					
13.ii	0	2	0	0	2
12.iv	4	30	4	1	39
16.iv	13	59	5	1	78
20.iv	19	63	8	1	91
22.iv	19	43	27	2	91
26.iv	26	11	22	39	98
28.iv	28	11	11	50	100
30.iv	28	11	10	51	100
3.v	32	13	10	51	106
7(*b*) 45 eggs kept moist:					
12.iv	1	19	0	0	20
16.iv	1	29	0	0	30
20.iv	5	12	13	7	37
22.iv	6	12	7	14	39
26.iv	6	8	9	20	43
8.v	4	6	7	26	43

In this table, eggs with central eye-spots have been classified as at stage (1). No further development ensued up the end of May. The rather early hatching of eggs kept at outdoor temperatures might have been caused in part by their having been kept under glass, but was probably largely due to general climatic conditions rather than experimental; the spring of 1948 was an " early " one, other insects also appearing earlier than in 1947.

terminable merely by a rise of temperature is indicated by the results of a series of preliminary experiments outlined below.

Experimental methods.—Eggs were placed in Petri dishes, either directly or after preliminary treatment as described below, some on dry filter-paper, others on moist glass wool, and left either at a constant temperature of 25° C. or at outdoor temperatures. Inspection to note progress of embryonic development was made on alternate days.

Those eggs given initial exposure to —8° C. or —4° C. were kept dry in a refrigerator for the appropriate periods of time. Eggs soaked in xylol or in water were kept immersed by weighing down with filter-paper. The xylol-treated eggs were soaked in pure xylol for 45 minutes (following Slifer's (1946) method), subsequently given several washings in distilled water, and then left to soak in water for 24 hours before being transferred to the Petri dishes.

Stages in development.—Attempts to remove the chorion without damaging the egg were unsuccessful. However, even in the intact egg certain stages of embryonic development are clearly distinguishable in virtue of associated pigment formations showing through the chorion. Four obvious stages are definable which can be used in experiments as criteria of resumed development:

(1) A pair of small red eye spots at the posterior end of the egg. At this stage their small size renders them liable to be overlooked without careful scrutiny. When first visible the eye-spots are somewhat dorsal, but during blastokinesis come to lie first postero-ventrally, then, moving forward along the ventral aspect of the egg, reach an antero-ventral position beneath the operculum.

(2) The eye-spots at the anterior (micropylar) end of the egg. Their ventral position is due to the deflection of the head beneath the thorax.

(3) The eye-spots considerably larger, and abdominal segmentation of the embryo indicated by a series of transverse red bands on the dorsal aspect of the egg. The long black setae characteristic of the first instar nymph are also clearly visible through the chorion.

(4) Hatching, with dehiscence of the operculum and emergence of the nymph.

Results of preliminary experiments.—In Table XII are given the total numbers and percentages of eggs developing and hatching under the different treatments used. Results are given up to the end of May, 1948. Speed of development is considered in the course of the discussion.

Discussion and Conclusions :

Experimental results so far obtained, although incomplete, already give some indication of the nature of the effect of several factors on the diapause, and also point the way to improvements in method and to further lines of investigation. In some of the experiments the deleterious effects of excessive moisture and, in the later stages of development, of desiccation at low R.H. and high t°, have to a certain extent masked the effects of other factors.

It is seen that subjection to a high temperature (25° C.) is in itself incapable of breaking diapause in the great majority of the eggs. Normally, preliminary exposure to low (winter) temperatures (a well-known factor in the breaking of insect diapause) is necessary before the stimulus of higher (spring) temperatures can induce further development. This diapause-breaking effect of suitable low temperatures is shown by the results of four sets of experiments.

(1) After an initial exposure to a constant temperature of —4° C., 65 per cent. of the eggs developed and 27·5 per cent. hatched at 25° C. (development of 70 per cent. and hatching of 50 per cent. after exposure of 15 days to —4° C.). Similar exposure to —8° C., on the other hand, resulted in a percentage development and hatching not significantly greater than that attained at a constant temperature of 25° C. A retarding and even lethal effect of temperatures at such a low level is indicated.

(2) Exposure of eggs to outdoor temperatures in late autumn and early winter for periods of 35 and 47 days before transference to 25° C. resulted in development of 35 per cent. of the eggs and hatching of 5 per cent. The diapause-breaking effect of such treatment was considerably greater than that of constant exposure to 25° C., but less (though more rapid in the successful cases) than continued subjection to outdoor temperatures, and also less than in those eggs first kept at —4° C.

(3) Eggs first maintained during the winter at laboratory conditions of fluctuating temperatures (cold at night, warmer during the day), for longer periods than the preliminary outdoor treatment given those of group (2), showed 60 per cent. development and 28 per cent. hatching when transferred to dry conditions at 25° C. and 52 per cent. development and 0 per cent. hatching under moist conditions at this temperature.

(4) Of eggs kept throughout at outdoor temperatures, 96·1 per cent. developed and 49·7 per cent. hatched in the spring.

The effect of cold in breaking diapause is evident in contrasting the results obtained in these four groups with those for eggs maintained at a constant temperature of 25° C. (6·7 per cent. showing development, 2·3 per cent. hatched). In only two of the four eggs recorded as hatched did the nymph completely emerge from the shell (see footnote, Table XII). Moreover, in all except one of the 12 eggs that began development at 25° C., breaking of diapause occurred only after an exposure of from three to seven months, and so must have been due in these few eggs to the intervention of some factor other than high temperature *per se*. Resumption of development after the breaking of diapause by cold, on the other hand, ensued at 25° C. after a matter of a few days. With those eggs exposed to outdoor temperatures, development, as occurs normally in the field, began only with the onset of warmer weather in spring.

There obviously are minimum effective periods of exposure to low temperatures, but quantitative experiments on this point have not been made. It has been seen that exposure to outdoor temperatures in late autumn for 7 days (12–19.xi) and for 14 days (12–26.xi) was insufficient to break diapause, whereas periods of 35 and 47 days, extending to the middle and end of December respectively, were effective in a significant number of eggs. It was also seen that exposure for as short a time as 7 days to a temperature consistently below F.P. (−4° C.) was sufficient to break diapause in 70 per cent. of the eggs treated, and that there was no increase in percentage development with longer exposures at this temperature. There is an indication of an increase in percentage hatching with an exposure of 15 days and a decrease with periods of still longer duration, but the comparatively small numbers of eggs used for this series of experiments and the paucity of knowledge of other factors influencing mortality and development make any further conclusions based on these data uncertain.

From the experiments on eggs maintained at 25° C. it would seem that very rarely (in these experiments, once in 175 cases) an egg may be non-diapausing (development to stage (3) after 12 days), and, further, that after several months diapause may be broken in a small proportion of eggs (11 out of 175) without exposure to low temperatures. This is discussed below, but there is no conclusive evidence of what factors might be involved in such instances.

Evidently both the breaking of diapause and at least the earlier stages of embryonic development can proceed within quite wide ranges of temperature fluctuation, provided an adequate total exposure to low or high temperatures respectively is given. In experiment 3 (*a*) eggs were subjected to alternating periods of low and considerably higher temperatures. Not only was diapause broken by this treatment in 60 per cent. of the eggs, but also subsequent development had evidently occurred. On transference to 25° C., one egg hatched after 4 days and 3 others by the sixth day. In no other experiments did an egg hatch any sooner than 10 days after transfer to 25° C. Development generally at this temperature was more rapid in experiment 3(*a*) than in any other.

It is possible that in some experiments in which diapause was only partially eliminated by cold, this may have been because the eggs concerned were not at a suitable stage of embryonic development at the time of exposure, and this question needs to be settled by further experiment. Andrewartha (1943) found that in the egg of the grasshopper *Austroicetes cruciata* Saussure exposure to low temperature when the embryo was not at a suitable stage of development resulted in only partial elimination of diapause, and that after removal to a favourable high temperature there was abnormal embryonic growth but development was not completed.

Immersion of the eggs in xylol seems also to have a diapause-breaking effect.

After such treatment a total of 26 per cent. of the eggs showed development at 25° C.; 8 per cent. were developing after 13 days (10.xi), 12 per cent. after 27 days (24.xi), and 20 per cent. after 66 days (2.i), the last date being 13 weeks earlier than that at which development was first noted in any except 2 eggs of 155 kept at outdoor temperatures. None of the eggs, however, hatched. Of 24 eggs similarly treated with xylol, but then transferred to outdoor temperatures, 91·7 per cent. developed and 87·5 per cent. hatched, at the same time in spring as those eggs kept at outdoor temperatures without such previous treatment. From a comparison of these two results it seems possible that, even after washing, some xylol may persist in the egg, and that if development begins before this is lost the xylol may retard development of the egg and eventually kill it. Further, the xylol-treated eggs after transference to 25° C. were kept moist, the deleterious effects of excessive moisture not being realised when the experiment was set up. This test needs to be repeated under dry conditions at 25° C.

Andrewartha (1943) concluded that the influence of low temperature on the elimination of diapause in the eggs of the Acridiid *Austroicetes cruciata* was due chiefly to changes which occurred in the yolk during exposure to cold, making it suitable for the nourishment of the embryo and also allowing blastokinesis to proceed. Pepper (1937) had put forward a similar suggestion to explain the action of dilute solutions of xylol and other chemicals in breaking diapause in the larvae of the Pyralid *Loxostege sticticalis* L., development, according to his theory, being resumed following activation of fat-digesting enzymes. It seems not improbable that the diapause-breaking effect of xylol might be due to some such modification of the yolk in the eggs of *Myrmus*. Such a hypothesis might also explain the development of an occasional non-diapausing egg soon after exposure to high temperature, on the supposition that the yolk, in these rare instances, was already in an assimilable condition and favourable to blastokinesis. Further, the development of a small proportion of the eggs after several months at a constant high temperature might depend on some slow process of yolk transformation induced either directly by such temperatures or by other factors as yet undetermined. Slifer (1946) showed that the action of xylol and other solvents in preventing or breaking diapause in the eggs of the Acridiid *Melanoplus differentialis* was probably due to the dissolving of a waxy substance from the hydropylar area of the egg cuticle, allowing the entrance of water necessary for further embryonic development. She pointed out the possibility that exposure to low temperature broke diapause by altering the structure of this waxy layer and so increasing its permeability. Since the eggs of *M. miriformis* can complete development and hatch without the entry of water from outside, it seems that a comparable mechanism cannot be involved in this insect.

This independence of an exterior source of water is shown by the results of experiment (7). There is, however, no doubt an optimum range of R.H. for developing and hatching which seems most unlikely to have been maintained at all times during experiments. On the one hand, it appears that prolonged exposure to saturated conditions has an inhibitory and even a lethal effect. This is indicated most clearly in experiment (3), in which eggs kept moist developed more slowly than those kept dry, all the former, moreover, failing to hatch, whereas 28 per cent. of the latter hatched. It seems most probable that in some experiments the deleterious influence of excessive moisture has to a certain extent masked the diapause-breaking effects of low temperature and xylol. On the other hand, there was death of developing eggs from desiccation (e.g., in experiment (7*a*)) at humidities probably lower than those normally obtaining in the field. Such mortality was due to excessive loss of water from the eggs rather than to absence of water intake. It would be necessary to determine the optimum R.H. range for normal development before making further experiments to elucidate the details of the diapause mechanism in *Myrmus* eggs.

In their water requirements, the eggs of *Myrmus* probably differ from most other diapausing eggs of Heteroptera and indeed, so far as can be gathered from the literature, of insects generally. Among the Heteroptera, the laying of exposed eggs, attached externally to plants, occurs throughout the Pentatomidae, but in no British species of this family are the eggs known to overwinter. The oviposition habits of the British Coreidae, where recorded, are similar, but the eggs are known to overwinter only in *Myrmus miriformis* (Fallén) and *Chorosoma schillingii* (Schummel) Schilling. The eggs of the latter species are very similar in external appearance to those of *Myrmus*, and might be expected to show similar hibernating characteristics. Of other eggs that do hibernate, all, so far as recorded, are laid in moist situations, usually inserted into plant tissues or between closely adjacent plant organs (e.g., many species of Mirids, some Nabids, and apparently some Tingitids, e.g., *Dictyonota strichnocera* Fieber (Butler, 1923)). It is likely, therefore, that the detailed mechanism of diapause elimination is somewhat anomalous in the eggs of *M. miriformis*.

(6) *Summary.*

1. *Myrmus miriformis* (Fallén) inhabits "grass-heath" areas in which shallow-rooting grasses such as *Agrostis canina*, *Festuca ovina*, and *Sieglingia decumbens* predominate, interspersed with calcifuges like sheep's sorrel and *Calluna*.

2. The species, so far as observed, is entirely phytophagous and seems to show a preference for unripe grass-seeds.

3. Both sexes are dimorphic as regards wing-length, and the males also in colour. The brachypterous form is much the commoner (95 per cent. of all specimens captured). Whereas 77 per cent. of the males were of the brown colour form, all the females captured were green.

4. Adults emerge mainly during July, but also in smaller numbers towards the end of June and beginning of August.

5. Sexual maturation is rapid, and copulation, which is frequent and prolonged, occurs throughout the same months as oviposition.

6. There are seven ovarioles to each ovary. In each ovariole a small egg rudiment has already become separated in the fifth instar nymph. Only one egg ripens at a time in each ovariole, and there are never more than two other (much smaller) apical egg rudiments. Up to three ripe eggs may accumulate in each lateral oviduct before being laid. The presence of empty, dilated pedicel bases is an indication that ripe eggs have already left the ovarioles. There is no noticeable formation of corpora lutea.

7. The fat-body, well developed at emergence and even in the fifth instar nymphs, is gradually depleted in the course of egg-production, and by the end of the oviposition period most of the fat lobules are exhausted.

8. The species is univoltine and overwinters only in the egg stage.

9. Eggs are laid, attached usually to grass or heath leaves, during July,

August and September, and undergo an obligatory diapause for 8–10 months, hatching during the following May.

10. Exposure of eggs to low temperatures is normally necessary to break diapause before higher temperatures will initiate further development.

11. There is indication that immersion of eggs in xylol has a similar effect in breaking diapause.

12. The chorion is hydrofuge and impermeable to water. The egg, at laying, contains all the water necessary for complete embryonic development and hatching.

VII. General Summary.

1. The types of reproductive cycle occurring in the Heteroptera are described and classified.

2. The Mirid *Stenodema laevigatum* (L.) is univoltine, the longlived adults of both sexes overwintering, with copulation and oviposition delayed until spring. There is a large fat-body formed and considerable loss of water content in both sexes before winter, and " gonotrophic dissociation " is complete in the females, which undergo an obligatory diapause in ovarian development.

3. The Mirid *Notostira erratica* (L.) is bivoltine. The adults of the first (summer) generation are comparatively short-lived, do not accumulate large fat reserves, and undergo rapid sexual maturation. The females of the second (autumn) generation are long-lived as adults and hibernate, producing eggs in spring, but there is not the same degree of " gonotrophic dissociation " as in *Stenodema*, fat storage and reduction in water content being considerably smaller and egg rudiments being formed in autumn. High temperatures can cause resumption of reproductive development at any time. The males of this generation, which accumulate little fat and do not lose water, soon become sexually active, fertilising the females in autumn and not surviving the winter. Structural differences between the two generations are discussed.

4. The Coreid *Myrmus miriformis* (Fallén) is univoltine, with a relatively short adult life in both sexes. The eggs, which at laying contain all the water necessary for complete embryonic development, overwinter, undergoing an obligatory diapause of some 8–10 months, which is broken by low temperatures, and hatching in late spring.

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NOTES ON THE BIOLOGY OF *MELAMPSALTA CRUENTATA* FABRICIUS (HEMIPTERA-HOMOPTERA: CICADIDAE), WITH SPECIAL REFERENCE TO THE NYMPHAL STAGES.[1]

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(*Entomological Research Station, D.S.I.R., N.Z.*)

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(Read 7th May, 1952.)

With 1 Plate and 7 Text-figures.

Introduction.

Surprisingly little information on the life-history of Cicadas is to be found in the literature, in view of the attention which these insects have attracted. The work of Marlatt (1907), which includes a summary of previous contributions on the Periodical Cicada, is widely known. Myers (1929) has made a comprehensive survey of existing literature, and included information gained during the study of New Zealand species. The latter, together with short notes by Hudson (1890, 1892), and Potter (1896), comprise the information available on the biology of the New Zealand species.

In June of 1949 a survey of the insects associated with *Phormium*, a native fibre plant, was commenced at the Phormium Research Laboratory, Paiaka, for it was thought that insects might have some bearing on the question of a long recognised but obscure condition which has become known as "yellow leaf." Some suspicion at this stage had been placed upon Cicadas. The ease with which material could be obtained in this area provided an opportunity for the study of their biology.

The present investigation, which has been carried on over a period of a little more than one year, has produced nothing so spectacular as have the long-term projects summarised by Marlatt (1907). It is unlikely that any of our New Zealand species will show a longevity approaching that which apparently exists in the "Seventeen Year" species or "Periodical" Cicada. It is hoped that the present work, although necessarily limited, may suggest further avenues of investigation and throw a little light on the partly explained habits of these peculiar creatures.

The study of variation in the adult and of the genitalia and of nymphal populations has given no grounds for suspecting that two species are represented in the material examined.

Seasonal Appearance, Distribution, and Feeding Habits of the Adults.

It is not known to what degree the adult populations may vary in density from year to year. It is not suspected that this species may be absent in any one year.

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[1] Entomological Research Station Publication No. 11.

In the spring of 1949 the Cicada adults first appeared during the last week of November and their numbers increased gradually, the latest period during which they were seen being the last week of the following April. During the height of the summer adults of both sexes were present in large numbers on *Phormium tenax* Forst., *Carex ternaria* Forst. and *Festuca arundinacea* L., which, together with grasses, form the majority of the cover in the area studied. Field collections yielded more male than female adults, but this may be due in part to the greater protective coloration of the females, and the fact that only the males " sing " and thereby disclose their presence. Females are usually pale greenish, olivaceous, yellowish or ochreous (occasionally pink), while the males invariably possess a large amount of black, dark red, and brown.

Myers (1921) under the heading of distribution, writes as follows regarding this species : " . . . Probably generally distributed throughout the country at low levels." It is interesting to note that this is the only species not endemic. Goding and Froggatt (*Monograph of Australian Cicadidae*) record it from Adelaide and Victoria.

" This is the common Cicada of the open country from November to May. In contradistinction to the shrub-loving *M. muta*, it shows a decided preference for grass, herbage, and swamp vegetation on or near the ground. The species is extremely variable."

It is probable that the adult Cicada may feed on a variety of succulent plants. In captivity and in the field adults have been observed feeding on *Phormium* leaves. Grasses and *Carex* are considered to be additional food-plants.

OVIPOSITION SITES AND OVIPOSITION.

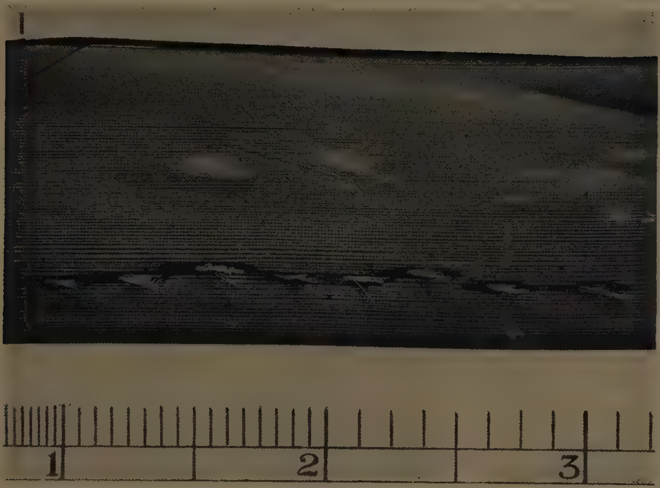
The act of oviposition has been described in detail by Marlatt (1907), Myers (1929) and others. The following are observations made on *M. cruentata :*

Oviposition Sites.

Most of the oviposition in the area studied occurred on three plants, namely, *Cordyline australis* Hook. f., *Phormium tenax* and *Festuca arundinacea*. *Arundo conspicua* Forst. and *Typha angustifolia* L. are used occasionally. In the selection of oviposition sites there appears to be a decided preference for monocotyledonous plants.

The egg measures approximately 1·7 mm. in length and 0·4 mm. in width, maintaining the latter except at the more pointed extremities. Eggs are deposited parallel to the length of the leaf, but lie at an angle with the surface. The implanting of numbers of these together necessitates a moderate thickness of tissue, and the fleshy parts of leaves, leaf bases and stems are usually selected. When shallower sites are used the eggs may remain exposed at their ends. In *Phormium* the fleshy sheathing leaf base is a favoured oviposition site. The blade, flower stalk and bract are occasionally used. In *Cordyline* the thicker basal third of the blade is usually selected. *Festuca* stems provide suitable depth for oviposition, and the Cicada often oviposits in these, leaving the eggs within the lumen. Later, when the stem has become dry, the eggs are dislodged and fall down inside the stem to accumulate above the node. In *Typha*

PLATE I.



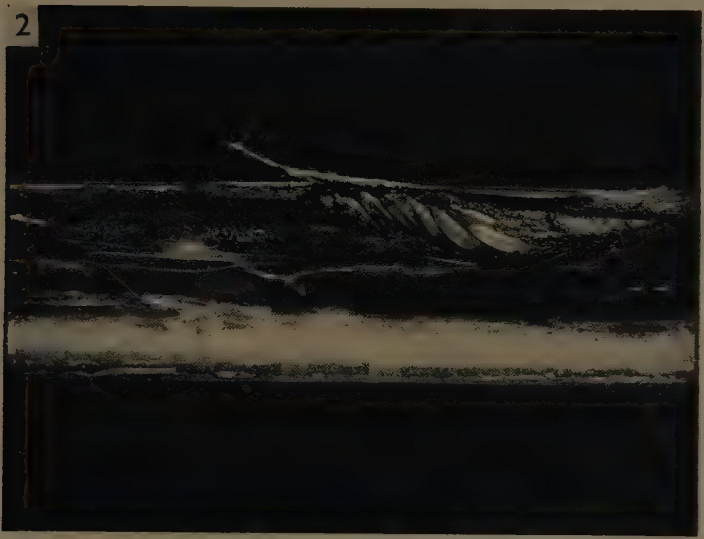


FIG.

1. Oviposition scars of *M. cruentata*.
2. Eggs of *M. cruentata* shown when the blade of *Phormium* is split by doubling back along the line of scars. Note the eyespots of developing embryos.

R. A. Cumber.

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eggs are placed within the large air-spaces of the leaves, while in *Arundo* the flowering stems are selected.

Perennial monocotyledons provide the more favoured site for oviposition, and it is probable that plants of this type are essential for maintaining high populations of *M. cruentata*.

Oviposition.

The act of oviposition occurs usually in warm still weather, when the songs of the males are very much in evidence. During oviposition, the abdomen of the female armed with the spear-like ovipositor works vigorously—almost furiously—in forming a pocket in the tissue for the reception of the eggs. The substrate selected is often tough and the act is a creditable one. In the process fibres are usually severed and remain with broken ends protruding from the oviposition scar.

Number of Egg-chambers Constructed and Eggs Laid.

On 25th January, 1950, a series of the current seasons oviposition scar groups was collected from *Phormium* and dissected to obtain information on number of eggs per scar, total eggs per group of scars, etc.. A typical group or row of scars is shown in Plate I, fig. 1, the eggs within the scar being shown in Plate I, fig. 2. In all, thirty-one oviposition scar groups were examined. Although the majority of these consisted of from two to six scars, as many as fifteen occurred together. The direct line of the scars and their spacing indicate, where large numbers of scars are present at the same site, whether they belong to one or more groups.

Occasionally two adjacent scars in the one group may approach each other so closely that it is difficult to determine to which chamber the eggs belong. Fairly commonly, the one scar gives access to two chambers which lie parallel and closely alongside one another. Some oviposition scar groups show mixtures of double and single chambers. The total number of eggs in the one group of scars varied from five (two of the three scars here had no eggs) to two hundred and sixty-eight eggs in the case of the fifteen scar group. The number of eggs per scar varied from nil to thirty-three, five to twenty eggs per chamber commonly being found.

Overwintering of the Egg and Emergence of the First Instar Nymph.

Marlatt (1907) has given the following information regarding " the growth and hatching of the eggs " in his work on the Periodical Cicada :

" The eggs remain in the twigs for six or seven weeks after being deposited. Professor Potter was one of the first to determine this rather unusually long egg period by marking certain egg clusters and watching them until the young larvae were disclosed. He reports that from eggs deposited on the 5th June he witnessed the hatching of the young on the 28th July. This statement is also corroborated by Doctor Smith. Miss Morris and others record a shorter period, and there is undoubtedly considerable variation due to weather conditions, but the normal period, as shown by the abundant records of this office and many observers, since those noted, ranges as stated from six to seven weeks. Some interesting instances have been noted of retarded development of eggs in plants yielding gummy exudations which had hermetically closed the nests from the air. Professor Riley notes a case of this kind where the eggs remained sound and unhatched until the end of the year, long after the trees had shed their foliage. Except in the extreme south, where all of the periods are somewhat earlier, the eggs are deposited chiefly in the month of June and most abundantly about the middle of this month, and the hatching period ranges from the middle of July to the first of August."

Myers (1929) in this connection writes as follows: "The time occupied in embryonic development is often very long. It seems usual for eggs laid in summer to hatch the same autumn or late summer . . . Pontedra believed hatching did not take place till the following season—which is true of certain egg-parasites with which Réaumur believed the Spanish naturalist confused the young Cicadas.

"In the case of *Melampsalta leptomera* in New Zealand, egg nests in marram grass collected on 31st December, 1923, gave young at dates varying from 15th to 22nd February, 1924, thus corresponding very closely with Marlatt's dates for the Periodical Cicada. The originally white eggs changed to salmon by 2nd February—thus rather late in the embryonic development . . . The date of laying of these *Melampsalta leptomera* eggs was unknown; but a second batch, laid in cocksfoot stems in captivity on 1st January, 1924, hatched almost *en masse* between 4 and 7 p.m. on 12th April—and this in spite of mould which had grown on the stems meanwhile."

During the autumn, winter and spring of 1949, oviposition scars from *Phormium*, *Cordyline* and *Festuca* were examined periodically in the field, and it was found during this period that in most cases the eggs were entire. It was apparent that either these eggs were parasitized, or that the majority of the nymphs did not emerge until the spring or summer following their deposition. The latter has proved to be the rule, although it was also found that some eggs were parasitized by a hymenopterous insect (Mymaridae). Early in January, 1950, a large amount of oviposition material laid during the previous season was collected and enclosed in glass tubes with cotton-wool stoppers. A limited number of nymphs emerged between 13th and 27th January.

During the autumn, winter and spring of 1950, a check was again made on Cicada eggs in the field. No trace of hatching was observed until 18th August, almost four months after the adult Cicadas had disappeared from the field. Twenty groups of oviposition scars from *Phormium* were examined on this date. In seventeen of these, all eggs, except an occasional outer shrivelled one, were entire and the groups showed variation in the stages of embryonic development. One group of scars contained empty eggs which could have produced nymphs. The other two groups of scars showed a mixture of empty eggs and emerging nymphs.

In the late spring and early summer a mixture of two seasons' eggs may be found in the field—a complicating factor which could easily have been overlooked if a periodical check had not been made during the preceding months. It is not impossible that a small number of eggs laid early in the summer may hatch out before midwinter, especially if mild autumn conditions prevail. (Myers' information on *M. leptomera* cited above may be affected by artificial conditions). But there can be no doubt that in the present species the majority of the eggs laid over-winter as such, and that the period of hatching out, like the period during which oviposition occurs, may extend over several months.

In the Periodical Cicada the eggs laid in each season are of a very uniform age in comparison with those laid by *M. cruentata*, for the adults of the former are present for five to six weeks as against five months in the latter species. The evidence that the egg stage in the Periodical Cicada occupies six to seven weeks, except in plants producing large amounts of gummy sap, seems to be well substantiated.

Myers (1921) has described *M. cruentata* as showing " a decided preference for grass, herbage and swamp vegetation." It appears that this species may oviposit on a range of plants including herbaceous dicotyledonous ones, but that the overwintering of the eggs as such makes perennial monocotyledons the more suitable, and where such are plentiful we may expect the largest populations.

In the future it is hoped that information on the period spent as an egg may be determined in other New Zealand species. It is probable that a similar condition will be found, as all belong to the genus *Melampsalta.*

The newly hatched nymph is remarkably active. After leaving the oviposition scar it falls to the ground, climbs down amongst the cover and enters the soil along the line of least resistance. Soon it may attain a depth of six inches or more.

THE NYMPHAL INSTARS.

The work of Marlatt (1907) gives detailed information on the nymphal instars of the Periodical Cicada. Some information on other species is given by Lyle (1910), Osborn and Metcalf (1920), Silvestri (1921) and Myers (1929).

From August, 1949, until July, 1950, samples of Cicada nymphs were collected at intervals from areas of plantation *Phormium.* During these collections the soil was carefully sifted so that the smaller stages would be represented as fully as possible. Each sample was taken from several separate sites in the area. This nymphal material was preserved in 80 per cent. alcohol. Subsequent analysis has provided information regarding number of instars, characters of the different instars, seasonal variation in the numbers of the different instars, and length of nymphal life. Most samples have comprised several hundred specimens.

Determination of the Number of Instars Present.

Three samples of nymphs were used in determining the number of instars present. The width of the head capsule (from side to side at the level of the eyes) of nymphs was measured. Measurements were made with a micrometer eyepiece (1 mm. = 23 units) and their frequency distributions determined. These are shown in Table I, which also indicates the size of the sample and date on which it was obtained. In these samples no first instar nymphs were obtained, so measurements are supplied from nymphs which were hatched out in captivity. Table II shows the increase between means of successive instars expressed as a ratio of the earlier instar. The peaks of the frequency distribution tend to be blunt, and this may be caused in part by the difference in size of the male and female nymphs. These measurements show clearly that five instars are present. Other characters which readily separate the different instars are indicated in the section on description of instars.

TABLE I.—*Frequency distribution of width of head capsules of Cicada nymphs.**

Date of sample.	Number of specimens.	6–7	8–9	10–11	12–13	14–15	16–17	18–19	20–21	22–24	25–28	29–35
18.x.49	223	.	.	.	.	.	.	2	.	2	20	8
5.xii.49	276	.	.	1	.	2	1	.	.	13	30	3
1.ii.50	243	.	.	1	14	18	11	1	.	10	60	17
Totals	742	4†	.	2	14	20	12	3	.	25	110	28

Date of sample.	36–40	41–45	46–50	51–60	61–70	71–80	81–90	91–100	101–110	111–120	>120
18.x.49	2	9	53	70	.	.	.	14	24	8	11
5.xii.49	2	38	90	40	.	.	.	26	16	13	1
1.ii.50	.	10	23	32	.	.	2	20	20	4	.
Totals	4	57	166	142	.	.	2	60	60	25	12

* 1 mm. = 23 units.

† From individuals hatched out in captivity.

TABLE II.—*Mean head widths of instars and ratio to preceding nymphal instar.*

Instar number.	Mean of instar.*	Ratio to preceding instar.
1	6·5	.
2	14·5	2·23
3	28·0	1·93
4	50·1	1·79
5	104·4	2·04

* 1 mm. = 23 units.

Marlatt (1907), referring to the number of nymphal instars, writes as follows:

" A careful study of the material collected in the course of the experiments described in the last section demonstrates the interesting fact that this species, in spite of its very long period of growth, presents the same number of adolescent stages as is found in insects which go through their entire development within a single year . . . But six distinct stages are found, four of which belong to the larval condition and two to the pupal. In other words, the larval and pupal changes in the Periodical Cicada are normal and are not increased by its long preparatory existence.

" It has been inferred hitherto, and notably by Professor Riley, that owing to the continuous use in burrowing, this species found it necessary to shed its skin and undergo a moulting once or twice a year, and instead of the normal number of changes or moults there were probably from twenty-five to thirty."

The species used in the present investigation indicates the presence of only five nymphal instars, the fifth instar corresponding with Marlatt's "first pupal stage." In the description of the second pupal stage Marlatt states: "This stage does not present any differences from the last except in the greater size of the specimens, which is noticeable in the relative dimensions of the parts hitherto measured for comparison." Marlatt does not indicate the number of the measurements upon which the above statement is founded. More extensive investigation of this point might show that a considerable variation in size occurs in the fifth instar nymphs, and that such a bimodal frequency distribution in size does not occur when a large sample of measurements is obtained.

TABLE III.—*Frequency distribution of width of head capsule of fifth instar Cicada nymphs.*

Width of head-capsule.	A. Autumn samples.		B. Spring samples.	
	Males.	Females.	Males.	Females.
<95	3	.	7	.
95–98	16	.	27	.
99–102	54	1	56	1
103–106	60	4	33	6
107–110	23	13	13	9
111–114	6	21	.	27
115–118	.	40	.	15
119–122	.	37	.	20
123–126	.	14	.	11
>126	.	2	.	4

* 1 mm. = 23 units.

The difference in size between "first and second pupal" instars described by Marlatt is not of the order which suggests that a moult has occurred. This, together with the absence of structural differences, makes the presence of a "second pupal stage" rather doubtful. Data put forward later (section on variation in adult populations) suggests other factors which may contribute to variation in nymphal size.

The question of these two pupal stages has been investigated in the present species, and no evidence for a second pupal stage has been found.

An autumn sample of 297 fifth instar nymphs, including both males and females and collected on 13th April, 1950, 9th May, 1950, and 30th May, 1950, was taken, and the widths of the head capsules (from side to side) were measured (1 mm. = 23 units). The frequency distribution of these measurements is shown in Table III under Section A. Section B shows similar measurements made on a spring sample of 229 specimens taken on 25th August, 1949, 18th October, 1949, and 1st November, 1949. The two samples, A and B, are given for a comparison of the pre- and post-adult emergence periods to eliminate the possibility of seasonal difference in fifth instar nymphal populations.

Description of Nymphal Instars.

In addition to the question of Marlatt's "second pupal instar" referred to above, there has been some difference of opinion regarding changes at the earliest stages of nymphal development. These are discussed by Myers (1929). These changes have been closely observed in *M. cruentata.*

When the Cicada emerges through a split in the outermost end of the egg it is enclosed in a thin, glistening, embryonic membrane which completely invests limbs, etc., every one separately, giving the embryo the appearance of an exarate pupa.[2] This membrane, however, tends to keep the appendages in a certain alignment, for they remain pressed against the body ventrally, reaching to its posterior end. This sharp-nosed, tapering form wriggles actively and obtains mobility in this manner. Its stream-lining must be of considerable advantage in wriggling its way out past the other tightly packed components of the egg chamber.

Once access to the exterior seems assured, the embryo casts this embryonic skin. The abdomen expands periodically with a peristaltic movement in an antero-posterior direction, which tends to push the membrane backwards and results in a posterior space between abdomen and embryonic skin. The posterior legs also appear to assist in pushing this skin backwards. These exertions result in tension anteriorly and the skin soon splits dorsally over the head and thorax. Within a few minutes the nymph has freed itself and the fine setae, previously completely covered, now become plainly visible. The process of hatching from the egg and casting the embryonic skin may take less than one and a half hours.

As already indicated, the number of nymphal instars was initially determined by ascertaining the frequency distribution of head-widths. Five well-defined peaks indicate the five instars. The size of the hard parts in successive instars is approximately doubled, so that the macroscopic separation of instars is, for the most part, a simple operation. The extremes of variation may be checked easily by resort to other characteristics about to be described. Nymphs belonging to instars 2 to 5 are present at all times, although the percentages of instars 2 and 3 may vary noticeably. The first instar was recovered from the soil in December and January sampling only.

The five instars are illustrated in figs. 1–5. Fig. 6 shows the inner aspect of the foreleg in each instar.

When a nymph hatches from the egg, or has recently moulted, the abdomen looks very small in comparison with the remaining hard parts, which do not increase in size during stadia. As the instar becomes older, the abdomen does increase in size until the picture is reversed. The overall size of a nymph does not vary greatly immediately before and after the moult, although the size of the hard parts may double. As indicated previously, no evidence for a sixth (" second pupal stage " of Marlatt) instar has been found.

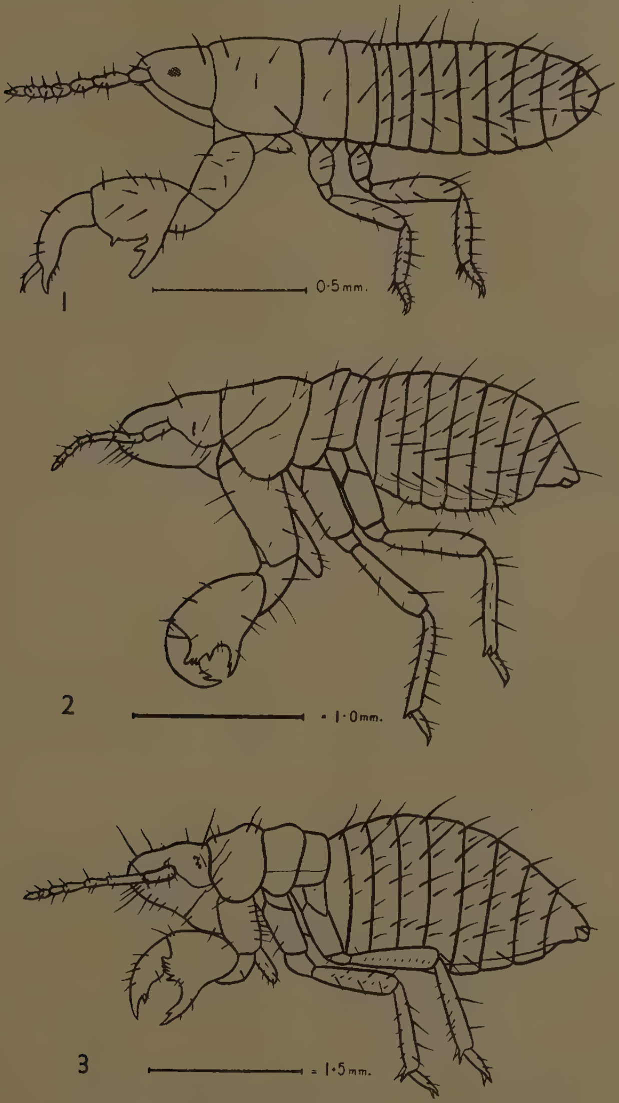
During the first and last nymphal instars the Cicada has a brief aerial existence, and at these times corresponding structural modifications are present. During the other stadia, which are spent entirely beneath the surface of the soil, such structures are extremely rudimentary.

Instar 1 (fig. 1).

The first instar nymph when newly hatched is light orange in colour and measures approximately 1·2 mm. in length (excluding antennae) and, although tapering anteriorly, presents a rather uniform width of about 0·4 mm. The nymph is clothed with numerous scattered hairs. The general form represents that of the later instars, although the appendages seem, in relation to other

---

[2] This pupal appearance will explain the error made by Costa (A., 1877), in his work on fruit trees pest in Italy, when he described the eggs of *Cicada orni* as the pupae of a new genus and species, *Macroprotopus oleae*, an injurious insect, of which the imago was the newly hatched cicada nymph.



Figs. 1–3.—*M. cruentata* Fabricius. Nymphal instars. (1) First. (2) Second. (3) Third.

stages, very large in comparison with the size of the body. The antennae, although seven-jointed as in all other instars, are relatively longer and straighter. A large red circular eyespot of some four or five darker, ill-defined components is strikingly different from the condition seen in subsequent instars. The forelegs, as in other instars, are characteristically modified. The tibia is relatively elongated, and bears a tarsus which arises well within the tip of the former and projects beyond it. At its extremity the tarsus is armed with two curved claws. Only in this and the final nymphal instar is a functional tarsus present in the forelegs. The inner prong of the distal portion of the tibia is reduced. A basal joint is present in functional tarsi of all instars. The femoral comb does not appear until the second instar, and the sub-apical tooth on the tibia until the third instar. During the first instar the nymph may reach a length of 2·0 mm.

Instar 2 (fig. 2).

During the second instar nymphs measure approximately 2·0 to 2·6 mm. in length. The eyespot, large and circular in the first instar, has now become a vertical line of dark spots. The nymph is more densely clothed with hairs. A tuft of hairs is present beneath the anterior end of the head. The antennae are distinctly angled. In the foreleg the femur possesses a rudimentary comb of three teeth, the uppermost of which is the broadest and projects beyond the others. The central tooth on the femur is more pronounced. The tarsus is reduced to a tiny rudiment now situated level with the inner prong of the bifid extremity of the tibia. The spines on the inner surface of the femur have increased in number and continue to do so in successive instars.

Instar 3 (fig. 3).

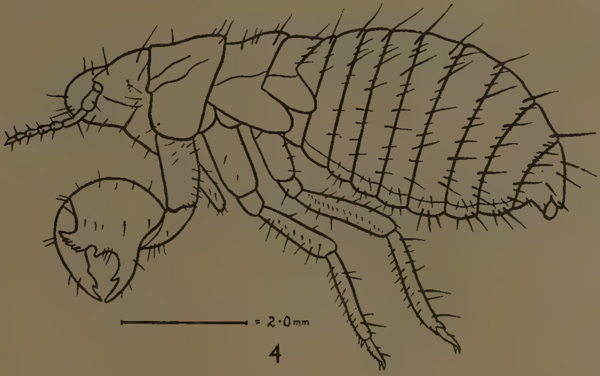
Third instar nymphs measure approximately 2·2 to 5·5 mm. in length. The eyespot is still further dispersed and is now composed of about four separated spots. The femoral comb has four teeth, the upper one being wide and prominent. The anterior tibia has a small tooth within the blunt sub-apical one. The anterior tarsus is rudimentary as in the previous instar. The middle and posterior femora possess rows of small spines along their inner margins.

Instar 4 (fig. 4).

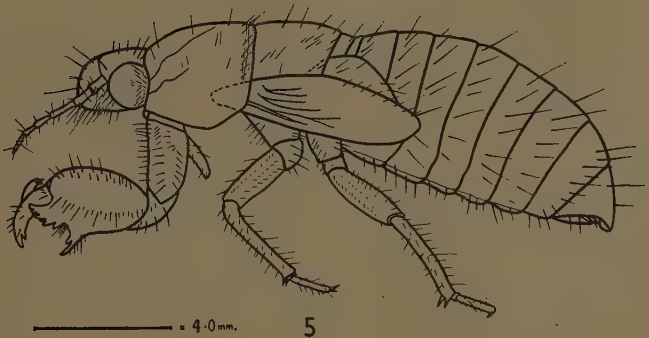
Fourth instar nymphs measure approximately 6·0 to 11·0 mm. in length. The eyespot comprises a group of some four to six scattered dots. The femoral comb is composed of five teeth including the large upper one. The tibial tooth with the sub-apical one is not so prominent as in instar 3. Spines and hairs are increased in number and size. Rudimentary wing cases are plainly discernible and the sexes may be readily distinguished.

Instar 5 (fig. 5).

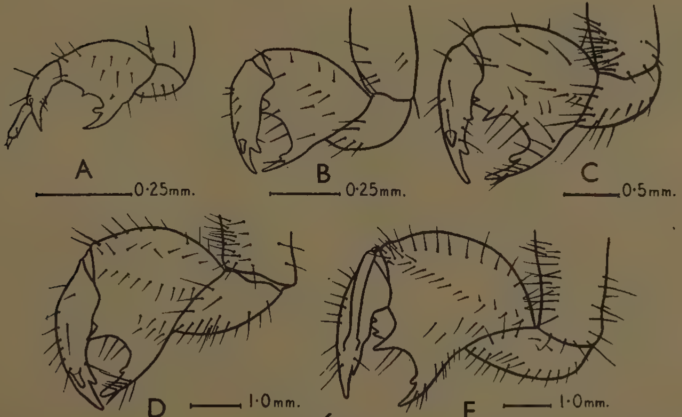
Fifth instar nymphs measure from 11 to 20 mm. in length. Wing cases extend to the third abdominal segment. Eye prominences are well rounded. Eyespots consist of from four to six black spots, but the position of the group may vary as explained below. The femoral comb is composed of six teeth,



4



5


A
0·25mm.
B
0·25mm.
C
0·5mm.
D
1·0mm.
E
1·0mm.

6

FIGS. 4–6.—*M. cruentata* Fabricius. (4) Fourth nymphal instar. (5) Fifth nymphal instar. (6) Inner view of foreleg in each nymphal instar.

The tooth within the sub-apical tibial one is now reduced to a ridge. The anterior tarsi are again well developed and lie folded along the inner face of the tibiae, almost equalling them in length. The tarsus is composed of a small basal joint, the second main joint, and two apical claws.

In Marlatt's account of the " pupal " stages, which correspond to the fifth instar above, he states that eyespots are " entirely wanting." Further investigation will probably show that eyespots are present in the normal position during the early period of the instar, and that these later travel posteriorly beneath the double row of hairs on the eye prominences, to lie at the posterior margin of the pigmented eye. This is clearly demonstrated in the present species. Fig. 7 shows the eyespots at different positions during their movement.

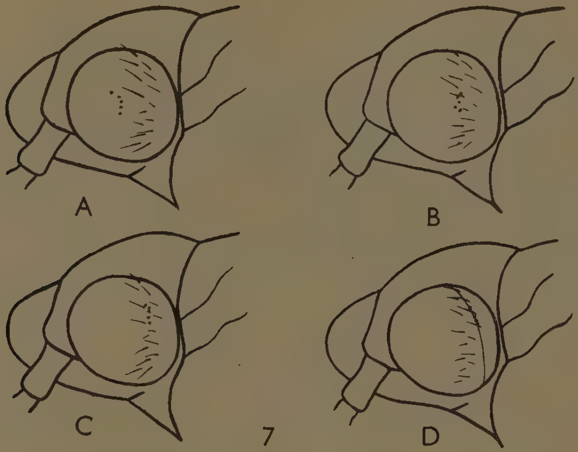


Fig. 7.—*M. cruentata* Fabricius. The migration of the eye spots in the final instar nymph.

Approximately when pigment begins to appear at the anterior inner margins of the eye prominences the eyespots commence this migration and appear to be swept back by the hind margin of the pigmenting eye, which seems to rotate backwards as it pigments.

Seasonal Variation in the Numbers of the Different Instars Present.

From August, 1949, until July, 1950, a regular sampling of nymphs was carried out, and it was hoped that subsequent analysis would provide information on seasonal changes in the numbers of the different instars present. Such an analysis, however, is complicated by several factors which necessitate a very large sampling if reliable data are to be obtained. Firstly, *M. cruentata* has a nymphal cycle occupying more than one year, so that at any time one may be dealing with one or more generations of insects. Secondly, in the area studied there appeared to be either a migration of the larger instars towards the base of the *Phormium* bush, or there was a higher mortality amongst the later instars below the grass away from the base of the plant. To illustrate the population variation, in one instance, two samples (200–300 specimens), each collected from several spots within the trial area on the same day, showed a difference of 10 per cent. in the numbers of the more plentiful instars.

Table IV shows the percentages of the different instars obtained beneath the *Phormium* plants, compared with percentages obtained beneath grass approximately two feet distant from the base of the plants. It is conceivable that the larger nymph, having more exacting food requirements, should find the large succulent roots of *Phormium* a more satisfactory source of food than the finer adventitious roots of grasses, especially as the latter tend to suffer during the height of summer. It is possible that the latter roots are satisfactory for the less exacting earlier nymphal stages.

Much of the *Phormium* in the area studied was cut in August, 1948, but considerable leaf had grown by the following summer. This cutting may have affected the nymphal populations.

Table IV.—*Analysis of nymphal population beneath* Phormium *bushes and beneath adjacent herbage.*

Instar.	Percentages.					Total specimens.
	1.	2.	3.	4.	5.	
Samples (9.v.50)						
Beneath *Phormium* bushes			21	44	35	85
Beneath adjacent herbage		10	79	8	3	140
Samples (30.v.50)						
Beneath *Phormium* bushes		3	29	47	21	147
Beneath adjacent herbage		4	55	29	12	228

An attempt was made to obtain information on the periods occupied by instars by use of cages. The placing of field cages over grass between *Phormium* bushes showed that adults emerge from herbage root-feeding sites. Sunken boxes containing soil covered with grass sods have been set up and nymphs of known instars have been added. It will be necessary to wait one or more years before definite information is available from this source.

It is possible that, in spite of difficulties in sampling the nymphal populations, the grouping of samples may provide data based on sufficient numbers to provide some indication of seasonal changes. This will be correlated with data from the nymphal changes in cages when the results of the latter are available. Table V shows the percentages of the different instars present in samples taken during 1949–50.

In the period April to July few of the nymphs have not reached the third instar, and by October the majority have reached the fourth instar. From August to January at least 70 per cent. (allowing 10 per cent. for missing of smaller instars during sampling) of the nymphs belong to the fourth and fifth instars. Since fifth instar nymphs are present at all times they must overwinter as such.

A period of approximately one year is spent in the egg stage, and it appears that the nymph hatching out in spring or summer may reach the third or fourth instar by the following spring or summer. During the summer of the second year the fifth instar is probably reached, the adult emerging in the following summer, this being almost three years after the egg was laid, and two years after the first instar nymph hatched out. The relatively small numbers of first and second instar nymphs found in summer will be due partly to their small size and the ease with which they may be overlooked during sampling. Also, it is probable that the first two instars are passed through relatively quickly.

TABLE V.—*Instar percentages in samples taken during* 1949–50.

Dates of samples taken .	1.viii.49 25.viii.49 18.x.49	1.xi.49 6.xii.49 11.i.50	1.ii.50 17.ii.50 22.iii.50	13.iv.50 9.v.50	30.v.50 14.vii.50
Total specimens . .	628	925	740	921	446
Instar.	Percentages.				
1	.	0·3	.	.	.
2	0·8	7·2	9·9	1·6	3·6
3	11·4	12·2	32·1	29·7	41·6
4	55·8	46·3	29·0	31·2	32·7
5	32·0	34·0	29·0	37·5	22·1

Resistance to Submergence.

Marlatt (1907) records instances in which nymphs in the soil remained quite unharmed, although water covered the soil above them for long periods. He suggested that the impervious nature of the soil might explain this. The artificial flooding of a portion of a *Phormium* area has shown that the nymphs may survive for a period of at least four weeks even though the soil in which their burrows lie is saturated.

It is well known that the walls of the burrows are smooth and tightly packed. The liquid faeces, which is passed in large amounts, no doubt helps in the agglutination of the soil particles.

In addition to the protection afforded by the walls of the cell, the nymph is itself able to withstand days of submergence. The abdominal spiracles in instars 2 to 5 lie on the inner side of the pleural flaps. The abdomen is arched and concave beneath. Projecting into this concavity is a series of long hairs. If a Cicada nymph is immersed in water an air bubble covers the lower surface of the abdomen and, no doubt, the nymph can draw on this oxygen supply for a considerable period.

THE VARIATION IN SIZE OF THE ADULT CICADAS.

Marlatt (1907) has discussed the occurrence of the Periodical Cicada in two distinct size forms. The smaller form was described as a distinct species in 1857 by Fisher. The smaller form is approximately two-thirds of the size of the larger one. The two show close anatomical similarities, but vary in coloration, song, and time of appearance. Osborn (1902) studied the variation in size and other characteristics of the large and small forms using a series of 800 specimens taken at random from various localities, and he decided that the colour variation and size differences were significant, although these overlapped. The mating of the smaller with the larger form apparently has not been observed.

During the summer of 1949–50 adult Cicadas were collected at intervals from the area being studied, and these were kept in 70 per cent. alcohol. By the end of the flight season the sample comprised 143 males and 74 females. The variation in size in each sex was determined by measuring the head-width (from side to side) at the level of the eyes. Measurements were made with a micrometer eyepiece (1 mm. = 23 units). The frequency distribution of measurements so obtained showed a slight tendency towards bimodality in both sexes, and it was considered that there might be some factor other than sampling error involved. The frequency distribution of head widths is shown in Table VI.

TABLE VI.—*Frequency distribution of head-widths* of adult Cicadas.*

Head measurement	96	97	98	99	100	101	102	103	104	105	106	107	108	109	110	111	112	113	114	115	116	117	118
Frequency:—																							
Males	1	.	1	.	.	3	3	.	1	3	3	8	8	9	8	12	15	15	7	8	6	12	7
Females	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	1	1	.	2

Head measurement	119	120	121	122	123	124	125	126	127	128	129	130	131	132	133	134	135	136	137	138	139	140
Frequency:—																						
Males	6	5	2	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Females	1	.	1	6	3	7	1	8	6	1	4	3	5	5	7	5	3	1	1	1	.	1

* 1 mm. = 23 units.

TABLE VII.—*Size differences* in fifth instar Cicada nymphs found beneath* Phormium *and associated pasture.*

	Number of specimens.	Mean head width.	σ.
Males from *Phormium*	24	103·4	4·26
Males from pasture	24	98·3	3·59
Females from *Phormium*	30	118·5	4·19
Females from pasture	30	107·9	4·59

* 1 mm. = 23 units.

A further check on genitalia was made to ensure that two species were not involved. Coloration was studied, for in the males the smaller individuals show a tendency towards an increase in the extent of the dark coloration.

The study of the fifth instar nymphal population may throw some light on the question. The sampling area is for the greater part covered with rows of *Phormium* bushes interspersed with cover of mixed grasses. Cicada nymphal populations are present under both *Phormium* and pasture, but the Cicadas beneath the *Phormium* appeared to be the more robust. This difference in size has been measured and is shown in Table VII. The sampling sites (beneath

Phormium bushes and beneath pasture) were within a few feet of each other, and the differences in size of individuals in the samples are highly significant ($P < \cdot 001$) for both sexes.

It is difficult to evaluate the implications of these results. However, they provide a possible explanation for the tendency towards bimodality in the size of the adults. In the past it has been generally agreed that both nymphal and adult populations (particularly the former) do not travel any distance in the one generation, and here we may have further evidence for this.

In the area studied it is probable that the greater part of successful oviposition takes place on the *Phormium* bushes, but that the first nymphal instar may wander some distance from the base of the plant before it burrows down into the soil to begin its subterranean existence. Once it has burrowed down, its location appears to be static provided the terrain is not disturbed. Those nymphs which find themselves beneath the *Phormium* bushes are, in the long run, at a definite advantage over those which feed beneath the annual monocotyledonous pasture plants. This *Phormium* root association may be a common one for this species.

If one accepts the facts that smaller male individuals in the species show a fairly constant tendency in colour variation, and that in the present species a 10 per cent. variation in size may occur in nymphs which for about two or three years have been subject to different feeding conditions, what may be expected if nymphs which require a seventeen-year nymphal period are fed on sources of nutrition which are equally variable ? This aspect may bear some significance when attempting to explain the occurrence of the Periodical Cicada in the two apparently distinct size forms.

PARASITES AND COMMENSALS.

The Egg Stage.

A Hymenopterous Insect (Mymaridae), probably *Idiocentrus miris* Gahan.

A periodical inspection was made of Cicada oviposition scars to determine when the eggs hatched and the first instar nymphs entered the soil. In the course of these examinations it was found that a moderate percentage of the eggs contained embryos which belonged to a hymenopterous insect. Early in January a species of Mymaridae commenced hatching from oviposition scar material kept in glass tubes. At the same time the first instar nymphs were hatching from the Cicada eggs.

A large number of parasites were hatched out and mating and further parasitization of egg material supplied were observed. The unfolding of the long oviposition sheath and the subsequent extrusion of the ovipositor gave the insect a remarkably lengthy instrument for reaching the host eggs, many of which lay at quite a distance from the entrance to the oviposition scar. As many as eight of the outermost eggs in a scar containing twelve Cicada eggs have been noted as parasitized, the state of development of the parasite in the egg being progressively retarded deeper and deeper from the opening of the scar (as, indeed, is the state of development in unparasitized eggs).

The emergence, during the last week of January, of the adult Mymarid from the current seasons Cicada eggs indicates that there is at least one adult generation of the parasite in addition to that which overwinters in the host egg.

It is possible to determine whether parasite or Cicada nymph has emerged from the eggs, for the former chews a circular emergence hole a fourth of the distance from the outermost end of the egg, whereas the Cicada nymph emerges through a split in the outer end of the egg. The female *I. miris* is described from the eggs of *M. leptomera.*

Mites and Fungi.

Mites of several species have been observed associated with Cicada eggs and their chambers but it is not known if any of these are parasitic. There also appears to be some fungal growth commonly associated with the oviposition scars in *Phormium.* This does not appear to be detrimental to the developing eggs.

The Nymphal Stages.

Larvae of the Carabidae (Coleoptera).

On many occasions newly killed fifth instar Cicada nymphs have been found together with large larvae of Carabidae. The latter gain entrance to the Cicada burrow and attack the abdomen of the nymph, subsequently eating out the contents of the entire body. The adults of two large carabid beetles, *Megadromus enysi* (Broun) and *Holcaspis ovatella* (Chaud.) var. *perbona* Broun (identified by E. S. Gourlay), occur in the soil about and beneath the *Phormium* bushes, and it is probable that the latter species is concerned here.

A Fungous Disease of the Nymphs.

Cunningham and Myers (1921) describe fungi belonging to the genus *Cordyceps* known to attack the nymphs of *M. cingulata* and possibly *M. cruentata.* The species *Cordyceps sinclairii* Berk., or an allied species, is present at Paiaka, and in some areas fifth instar nymphs are commonly infected. There may be a higher percentage of infection in areas which are periodically covered by flood waters.

The entire contents of the nymph are solidified by the mycelial mass or sclerotium, and, in the more advanced stages, the fungus covers the external surfaces.

A Collembolan Commensal.

Almost invariably one finds a small white Collembolan species in the burrows of the larger Cicada stages. It is probable that this insect derives some of its nutriment from the large amount of fluid passed by the Cicada nymph. Dr. J. T. Salmon has identified this species as *Folsomia novae-zealandiae* Salm.

The Adult.

Birds are known to feed upon Cicadas. North of Auckland kingfishers have been observed catching *M. cingulata.* At Paiaka sparrows are known to feed on *M. cruentata*, and it is probable that many other birds deplete their numbers. Spiders, too, take their toll.

SUMMARY.

The seasonal appearance, distribution and feeding habits of adults of *M. cruentata* Fabricius are discussed.

Oviposition sites, the number of eggs laid and the construction of egg chambers are described. It is shown that the majority of the eggs deposited during the adult flight season do not hatch out until the following spring or summer. This is in striking contrast to the corresponding six or seven-week period in the "Periodical," or "Seventeen year" Cicada of America.

The number of instars present has been determined. The emergence from the egg and the casting of an embryonic skin are described. The five instars are described and figured. An attempt has been made to determine the seasonal variation in the numbers of the different instars present in the soil.

Resistance to submergence during nymphal stages is discussed.

The variation in size of the adult Cicadas has been determined and reasons for the nature of this variation are suggested.

Notes on parasites and commensals are given.

APPENDIX.

Further Note on the Length of the Nymphal Life of *M. cruentata.*

Since the preparation of the original paper, information on the length of the nymphal life has become available through the caging of known instars. These results appended here are summarized in Table VIII. The nymphs were caged in boxes with wire-gauze covered holes, the boxes being let into pure sand. Boxes contained soil with grass sod coverings, sods being carefully checked for any included nymphs at the commencement of the experiment. Experimental nymphs were placed beneath the sods. The numbers of nymphs recovered after seventeen months are sufficient to enable conclusions to be drawn regarding the time taken for nymphal stadia.

TABLE VIII.—*Instar changes in caged nymphs of* M. cruentata.

Group.	Date set up.	Contents by instars.			Date examined.	Contents by instars.		
		2, 3.	4.	5.		3.	4.	5.
1	17.ii.50	55	0	0	16.vii.51	0	6	4
2	„	0	101	0	„	0	1	11
3	31.v.50	0	0	49	„	0	0	0

Information on time taken for earlier stadia was also obtained from the use of *Phormium* seedlings in pots. Cicadas oviposited on these during January, 1950. The experiment was set up in a glass-house, so that the development may have been speeded up slightly. The time taken from oviposition to second and third instars here was nearly twelve months, as both these instars were present at the roots when examination was made in late December, 1950.

Reference to Table VIII, group 2, shows that some 4th instar nymphs caged 17.ii.50 could not be expected to emerge as adults until the following summer, e.g., January, 1952. The period from 4th instar to adult may thus occupy 2 years. The pot experiments show a period of almost 1 year from oviposition to the 3rd instar. Summing these, the period from oviposition to the emergence of the adult would appear to occupy 3 years.

The absence of any nymphs remaining in group 3 cannot be regarded as proof that all 5th instar nymphs collected 31.v.50 had emerged, as the conditions of the experiment may not have suited this instar and there may have been heavy mortality. It may well be that, owing to the long oviposition season and the accompanying variation in stages of development in nymphs, those belonging to the last instar may have to spend a variable period as such. This might increase the period from oviposition to adult emergence to almost 3½ years for the late-hatched or less successful individuals, and the adult emergences from any one year's oviposition may thus occupy two adjacent years. Such a device is certainly a valuable one from the point of view of preservation of the species.

These caging experiments bear out the conclusions regarding the nymphal period which were obtained by a study of seasonal variation in numbers of the different nymphal instars present in the field.

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ON THE CLASSIFICATION OF THE TETTIGOMETRIDAE (HOMOPTERA: FULGOROIDEA).

By R. G. Fennah.

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With 10 Text-figures.

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Introduction.

The family Tettigometridae was erected by Germar (1821 : 6) for the reception of a single genus, *Tettigometra* Latreille, with the species *obliqua* Panzer and *virescens* Panzer, and was distinguished by characters of the head and by general body form.

Signoret (1866) and Fieber (1865, 1876) described new species from Europe in this genus, and in 1912 Oshanin catalogued the species from the Palaearctic Region. Walker (1851) described a new genus (*Isthmia* = *Hilda* Kirkaldy) from Sierra Leone, and Distant (1907) reviewed the species from South Africa. In 1903 Melichar described a new genus (*Egropa*) from the Philippines, and to it were added further species by Bierman (1907), Distant (1908, 1909, 1916) and Baker (1924).

In 1912 Schmidt (1912 : 459–462) described two new genera, *Megaloplastinx* and *Euphyonarthex*, and placed them in a new tribe, Megaloplastinxini, which he separated from the typical tribe (Tettigometrini) by the longer and relatively more slender legs.

The first comprehensive attempt to classify the family was that of Baker (1924), who divided it into three subfamilies, Tettigometrinae, Egropinae, and Megaloplastinxinae, separated principally by characters of the frons and vertex. The first of these included *Tettigometra*, together with Signoret's subgenera *Mitricephalus*, *Brachycephalus* and *Eurychila* recognised as separate genera; the second included *Hilda*, *Egropa*, *Mesegropa*, and *Nototettigometra*, and the third *Megaloplastinx*, *Euphyonarthex*, *Tembandumba* and *Raatzbrockmannia*.

Muir did not propose a classification of Tettigometridae, but made a fundamental contribution in drawing attention to the occurence in the family of two different types of male genitalia, the tettigometrine and the egropine (1923, 1924, 1930).

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A new classification of the family is proposed below, and has been developed along the line of approach suggested by Muir. In it three subfamilies are recognised, each based principally on a separate genitalic type, supported by external structural characters which appear to be significant. It has been found that the arrangement thus reached, which is believed to be natural, groups genera together quite differently from the classification of Baker: as a result the concept of the sub-family Egropinae discussed below bears little similarity to that hitherto accepted.

The writer's thanks are tendered to the authorities of the British Museum (Natural History) for the opportunity of examining material in the collection, and especially to Dr. W. E. China and Mr. R. J. Izzard for their ready assistance whenever it was sought.

2. KEY TO THE SUBFAMILIES OF TETTIGOMETRIDAE.

(1) (2) Vertex produced to extend in a cornice over base of frons; genital styles of male fused to form an elongate boat-shaped plate with a broad lobe on each side dorsally near base **Hildinae** subfam. n.

(2) (1) Vertex short or produced, rarely forming a strongly projecting cornice above frons . . . . (3)

(3) (4) Frons in adult distinctly umbonate in middle near frontoclypeal suture, or strongly medially carinate; a long upwardly-curved spine in this position in nymph. Genital styles with connecting membrane broad, bilobate or convex on hind margin . **Egropinae**

(4) (3) Frons not umbonate or extremely feebly so; head of nymph without a long upcurved medio-frontal spine; genital styles with connecting membrane very delicate, narrow, straight or concave on hind margin . . . . **Tettigometrinae**

3. EXTERNAL MORPHOLOGY.

The tettigometrid vertex is transverse, turbinate, parabolic, or triangular, with the disc usually flat or slightly hollowed, occasionally deeply excavate or, conversely, very slightly tumid (*Tettigometra brachycephala* Fieber). The frons is relatively broad and medially ecarinate (except in *Megaloplastinx*): a pair of fine lateral carinae bounds the frontal disc, either completely or from below the level of the ocelli to the frontoclypeal suture; they are almost straight and converge slightly distad. In some genera (*Hilda*) a crescentic transverse ridge may be developed in the region of the suture. There is no median ocellus: the lateral ocelli occupy a position on the genae anterior to, and slightly below, the eyes, and so closely adjacent to the lateral frontal carinae as to appear in most genera to lie directly above the basal end of the carina. In *Phalix*, described below, the ocelli lie just mesad of the apparent lateral carinae. This condition, in Fulgoroidea, is found only in Tettigometridae, where, however, it is not universal.

Almost as noteworthy is the unusual type of coordination between the form of the vertex and that of the frons. In most fulgoroid genera, as the vertex elongates, the frons elongates also; it retains a more or less plane surface and accommodates itself to the change by facing more ventrad: in Tettigometridae the subvertical apical half of the frons usually remains little altered, while the vertex advances independently, carrying the base of the frons forward with it.

The resulting profile may be not merely concave, but almost rectangulately so (*Raatzbrockmannia*, *Euphyonarthex*).

The clypeus is distinctive : as in myconine Achilidae the lateral pieces have turned to face anteriorly, and, in addition, have become tumid. The rostrum is of normal type, with the apical joint slightly longer than the subapical and rounded-conical at its tip, and usually terminates at some point between the mesotrochanters and the post-trochanters, though it may occasionally (*Tettigometra* subg. *Eurychila*) reach fully to the latter. The antennae show variation in length, but are comparatively uniform in structure, having a distinct ring-like basal joint and a cylindrical second joint, the latter studded conspicuously with exposed placoid sensillae, and bearing in a distinctly subapical position the minute third joint, which is prolonged in a closely " segmented " arista. It may be observed parenthetically that such segmentation of the arista is common, and possibly universal, in first-instar nymphal Fulgoroidea.

The eyes are of normal shape and size—though occasionally (some *Tettigometra*) the pigmented area appears rather small—and in dorsal view usually fit snugly into the sides of the head. In *Raatzbrockmannia* the eyes are more protuberant, while in *Megaloplastinx* and *Euphyonarthex* they are strikingly so. In most Tettigometridae the outline of the vertex and eyes, as seen from above, is carried almost without interruption to the lateral margin of the pronotum by the pronounced development of the side of the head which forms the posterior rim of the eye-socket : this is referred to below as the " post-ocellar callus." In *Tettigometra* a perfectly streamlined form of head and thorax has been attained at the expense of some loss of field of vision. The post-ocellar calli usually overhang the antennae closely and may cover them to the tip of the second joint. In *Megaloplastinx*, *Mesegropa*, *Euphyonarthex* and *Raatzbrockmannia* the antennae are remote from the eyes and project well out from the head.

The thorax is relatively unspecialised. Carinae are absent or only feebly indicated ; the tegulae are well developed. The post-trochanters rock in a mesad-(and slightly ventrad)—laterad (and slightly dorsad) direction. The post-tibiae are unarmed laterally and bear distally about seven short black-tipped spines. The hind tarsus of the adult bears between five and ten spines on its distal border, while the second joint invariably bears two, one at each lateral angle. In about half of the genera and most of the species of the family the legs are usually short and relatively stout : in the remainder, with extraordinary abruptness, they appear greatly elongated and slender in relation to the general bodily size, and the pro- and mesotibiae are slightly curved. In *Euphyonarthex* a sparse down of long, very fine silky setae is present on the inner aspect of the distal part of the protibiae.

The tegmina are usually of the macropterous type, but may be brachypterous ; they are always coriaceous and closely invest the body, and at most exceed it by very little. The costal margin near the base is inflected mesally. The venation is simple and reduced ; Sc and R are fused to near the node, M forks once, usually in the distal half, and Cu 1 is simple ; a claval suture is present in all macropterous tegmina, and the claval veins unite at or distad of the middle of the clavus. The veins are normally not prominent, and are often obscure distally, though occasionally they may be elevated. The dorsal surface is dull and covered with a bloom of wax ; occasionally (*Tettigometra*

(*Brachyceps*)) it is polished and distinctly punctate; in a few genera both surface textures are present in alternating fasciae.

The wings, when fully developed, are large and endowed with an ample posterior lobe. The venation is specialised, and Cu 1 is much thickened. With parallel examples from Issidae for comparison, it appears reasonable to presume that such specialisation has arisen in conformity with the requirement of folding the wing beneath the hard subconvex tegmen.

The abdomen is comparatively broad and moderately dorso-ventrally depressed. In the females of some species, and possibly in most, the intersegmental membrane can become substantially dilated, and the abdomen may expand until it exceeds the length of the macropterous tegmen. The abdominal spiracles, situated on lateral sclerites, are large and exposed.

In Tettigometrinae the anal segment of the male is short, subcylindrical and flattened below; in Hildinae the apical margin is greatly prolonged caudad in an upcurved spine. This modification recalls the similar, though much shorter, medial spine developed on the apical margin of the same segment in some Delphacini.

The pygofer is moderately short dorsally, but ventrally long, so that the genital foramen faces dorso-caudad. The ventral posterior margin is deeply and narrowly cleft in the middle line. The aedeagus and genital styles are wholly characteristic of the family, and fall into three main types.

In the tettigometrine type the aedeagus is suspended from the laterodorsal angles of the pygofer by a stirrup-shaped sclerite (fig. 2, D), and comprises a narrow sclerite, often with a dorsal median basal lobe (fig. 2, H, *l*), extended caudad below a large inflatable delicate membranous sac. The genital styles are paired, symmetrical, rod-like, and distally hamate, and are united by a thin unpigmented membrane which is transverse or concave on its posterior margin. The genital styles, as in all other Fulgoroidea with the exception of Derbidae, are connected by an apodeme to the base of the phallus.

In the second type, characteristic of Hildinae, the suspensory sclerite is longer than in Tettigometrinae, U-shaped and devoid of a transverse dorsal bar (i.e., not stirrup-shaped); it is more or less weakly united to the basal portion of the aedeagus, which assumes the form of a narrow sinuate sclerotised tube. At the distal extremity of this tube, on the obliquely lower aspect, there is a small membranous area. The genital styles are distinctive, and comprise only a pigmented trough-like sheath underlying the aedeagus, with a moderately large lobe on each side dorsally near the base.

In the tettigometrine genus *Mesohilda* (described below) occurs a most interesting transitional stage between the two preceding conditions. Here the basal suspension is stirrup-like, but forms an integral part of the phallus, and not a separate sclerite (fig. 4, E). The phallus is a narrow, simple tube with an apical pore (phallotreme). The pigmented sclerite which supports the more delicate part of the tube overlies the latter; in *Tettigometra* the sclerite which supports the aedeagal sac lies below it. The genital styles comprise a pair of rod-like, distally hooked limbs, as in *Tettigometra*, but these are united near their mid-points to an unpaired scoop-like sclerite which lies between them. This is pigmented in the distal region between the styles, but basally becomes thinner and transparent and forms a trough-like sheath underlying the aedeagus to the point of its suspension.

The third type, found in Egropinae, differs from the hildine principally in the aedeagus. Here the sclerotised basal part has become greatly inflated, almost bulbous, and is suspended at its basal angles. No U-shaped cavity is developed between the points of attachment. At the distal end of this inflated organ is a relatively small, trapezoidal, usually unpigmented lobe, into which passes the aedeagal duct. The genital styles are as in Tettigometrinae, but differ in that the transparent connecting membrane is broad and its posterior margin is bilobate.

The steps by which the genital styles have changed from the tettigometrine to the hildine form can be seen to have followed a course closely similar to the existing sequence tettigometrine–egropine–*Mesohilda*-hildine. Muir's conjecture (1924 : 221) that the lateral lobes of the hildine type correspond to the paired rod-like genital styles of *Tettigometra* is almost certainly correct.

The primitive aedeagus presumably took the form of a simple tube, of which the distal end was more or less flexible. This condition is similar to that in *Mesohilda*. The hildine aedeagus differs only in the suppression of the distal membranous portion, and the lengthening of the suspensory parts. In Egropinae the homologies are still evident : the swollen vesicle corresponds to the sclerotised pigmented part of the aedeagus of *Mesohilda*, and the transparent lobe at its distal end to the unpigmented distal portion. The homologies in *Tettigometra*, however, are not so clear : the superficial appearance suggests that the thin inflatable distal sac corresponds to the distal part of the primitive aedeagus. This may indeed be so ; but in view of the fact that in Hildinae and *Mesohilda* the pigmented sclerite overlies the distal membranous portion, whereas in Tettigometrinae it supports it from below, it is not possible to derive one type from the other.

In all three subfamilies the basal apodemes to which the muscles are attached and which connect the genital styles to the base of the aedeagus, are comparatively uniform and of normal structure. This is perhaps fortunate for the comparative morphologist, since, apart from these, the aedeagus of *Tettigometra* is of strikingly heteropterous form.

The female genitalia vary little, and are characterised by great reduction of the appendages. The pregenital sternite (VII) is relatively narrow (little broader than long), and distinctly medially excavate posteriorly (fig. 3, F). The lateral sclerites of the eighth segment are contiguous medially, and each bears at the anteromesal angle a small lobe. These lobes represent the first valvulae of the ovipositor, and, by reason of the thinness of the membrane which unites them to the margin of the lateral sclerite, are moderately flexible. A pair of short and narrow lobate processes is developed near the ventral points of junction between the eighth and ninth segments : these are the third valvulae. In the middle line, above the posterior margin of the pregenital sternite, lies a small stout quadrate sclerite, the subvaginal plate (fig. 3, F, H). The vagina, like the bursa copulatrix and spermatheca to which it leads, is membranous ; no sclerites are developed on the wall of either vagina or bursa copulatrix ; the latter is closely studded with ring-ornamentation.

4. TAXONOMIC AFFINITIES OF TETTIGOMETRIDAE.

Muir (1930 : 467), probably influenced by the combined characters of a bispinose second post-tarsal joint, the indication of a transverse groove across the hind angle of the mesonotum, and—in broad comparison—by the form of the aedeagus, suggested that Tettigometridae have more affinity with the Tropiduchid group of families than with the Cixiid group.

If it be assumed that the family is a natural member, possibly nearest to Tropiduchidae, of that group in which the second metatarsal joint bears two spines, then it may be claimed that Tettigometridae could have evolved in this group parallel to the superficially similar Gengidae in the ricaniid group. This would mean that the ocellar characters, the reduced lateral frontal carinae, the specialisation of the wings, the reduction of the female genitalia and the profound modification of those of the male are to be considered as casual and phylogenetically late modifications. This is a formidably large postulate, though not impossible. If, on the other hand, it be assumed that the bispinose condition of the second metatarsal joint has arisen twice in Fulgoroidea, and that Tettigometridae have no natural affinity with the " bispinose " and, as it were, phylogenetically post-cixiid group of families, then difficulties of another kind have to be faced.

Muir (1923 : 220, 221) expressed the view that " with the exception of the female genitalia . . . and the venation all the characters of this family are primitive," and listed the characters of the family which he considered to be cicadoidean : these are (1) a " segmented " antennal arista ; (2) no lateral carinae between ocelli and frons ; (3) lateral ocelli situated on frons ; (4) antennae closer together than eyes, and not distinctly below them ; (5) lorae visible in front view and forming a curve with " clypeal region "; (6) middle coxae allowing very little movement in a transverse direction ; (7) in some species, genital plates well developed and free. The first character is widespread in early nymphal fulgoroidea, if not universal ; the second does not hold in *Megaloplastinx*, and only applies to an obsolete, not an absent, structure ; the third character is not strictly correct, the ocelli usually appear to be situated at the basal end of the lateral carinae of the frons,[1] and not mesad of them. In *Megaloplastinx* the ocelli lie distinctly laterad of the lateral carinae ; only in *Phalix* do they lie mesad of the apparent lateral carina ; the fourth character is variable, and weak at best ; the fifth is found in myconine Achilidae ; as for the sixth, there is more difference between the mesocoxae of *Euphyonarthex* and *Phalix* than there is between *Phalix* and an issid such as *Scantinius bruchoides* Walker ; the last character is puzzling : a longitudinal median tract of the posterior ventral surface of the pygofer is more or less demarcated by a pair of grooves or wrinkles : laterad of this median tract the pygofer extends cauded in two lobes in some genera. These lobes are figured by Muir (1924 : 221, fig. 5, *gi*) as the "anterior gonapophyses" which, he claims, are " large, flat and projecting " in *Tettigometra*. The writer considers such homology dubious, but, accepting it for the present, would point out that the condition of the posterior ventral margin of the pygofer of the achilid *Rhotala* far surpasses anything in Tettigometridae as far as the presence of paired free apophyses is concerned.

As it appears to the writer there is not a single convincing cicadoidean character which is present in all Tettigometridae and absent from all other Fulgoroidea, and, in view of the evidently nymphal structure of the antennae, it may be that some of the supposedly primitive characters are neoteinic. It is perhaps worth noting that one of the unusual characters found in Hildinae, the presence of a velvety-black transverse band across the frons, with a small round spot of pure wax on each side of the middle line, is strikingly paralleled by the condition found in the eurybrachyid *Gelastopsis insignis* Kirkaldy.

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[1] The fact that the " frons " as recognised here is morphologically part of the vertex, and not homologous with the orthopterous frons, does not affect the argument.

5. SYSTEMATIC ARRANGEMENT.

Subfamily Tettigometrinae.

Frons in profile smooth, very slightly convex, flat, or shallowly concave; apical joint of rostrum about as long as subapical; antennae with second segment about two and a half times as long as first, not surpassing eyes, and separated from them by a thick callus. Profemora not reaching as far as sides of body, post-tibiae with 7–9 spines at apex, basal metatarsal joint with 8 spines at apex. Anal segment of male usually with lateroapical angles very shortly acute. Aedeagus more or less stirrup-like at point of suspension from pygofer. Genital styles rod-like, recurved at tip, with a narrow or laterally compressed membrane uniting them below aedeagus. Nymphs with head not anteriorly produced, in general similar to adult.

Key to Genera of Tettigometrinae.

(1) (2) Head with eyes wider than pronotum; frons about twice as broad as long; species more than 7 mm. long . . . . **Phalix** gen. n.
(2) (1) Head with eyes narrower than pronotum; frons not twice as broad as long; species less than 7 mm. long . . . . . . (3)
(3) (4) Post-ocellar calli in dorsal view with their posterior margin subparallel to posterior margin of eye; their width at lateral extremity at least equal to width at junction with margin of vertex . . . . **Tettigometra** Latreille
(4) (3) Post-ocellar calli in dorsal view with their posterior margin not parallel to posterior margin of eye; their width at lateral extremity much less than at junction with margin of vertex **Mesohilda** gen. n.

Tettigometra Latreille.

Latreille, 1804 : 312. Logotype, *Fulgora virescens* Panzer, 1799 : 12.

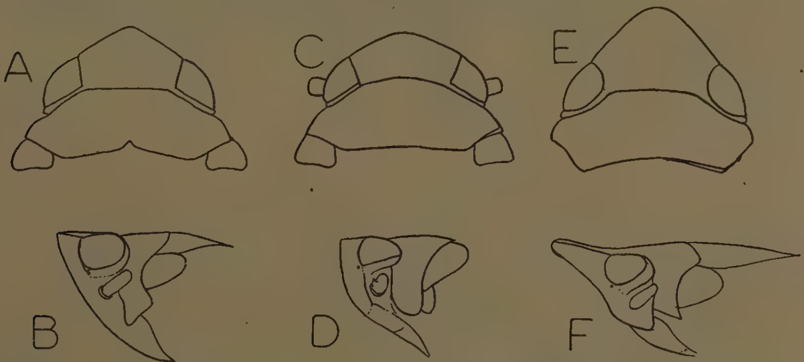

FIG. 1.—A, *Tettigometra virescens* (Panz.), vertex and pronotum; B, head in profile; C, *Brachyceps brachycephalus* (Fieb.), vertex and pronotum; D, head in profile. E, *Tettigometra sulphurea* Muls. and Rey, vertex and pronotum; F, head in profile.

Tettigometra virescens Panzer (fig. 1, A–B; fig. 2, H).

Fulgora virescens Panzer, 1799 : 12.

The figures are of a specimen in the British Museum (Natural History).

Apart from the character given in the key, males of species of this genus may be recognised by the form of the genitalia, described above. Lindberg (1948) has recently partially revised the genus and figured the genitalia of a number of species. He re-defines the subgenera *Tettigometra* Latreille, *Mitricephalus* Signoret, *Eurychila* Signoret, and *Brachyceps* Kirkaldy, and adds two more, *Micrometrina* Lindberg and *Macrometrina* Lindberg.

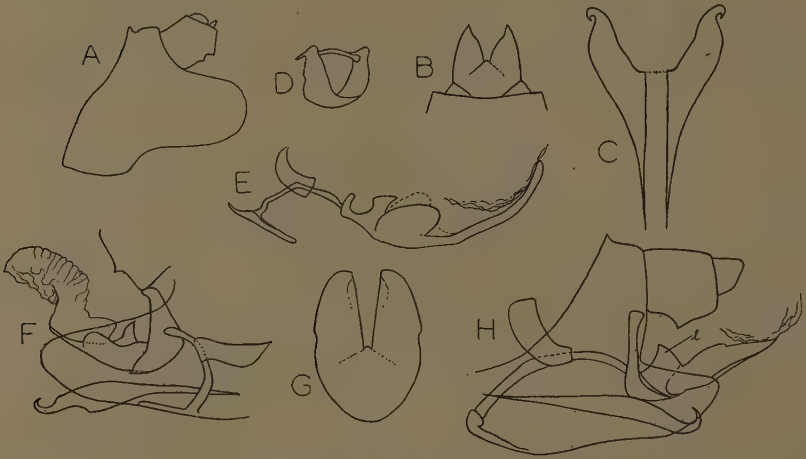

Fig. 2.—A, *Brachyceps brachycephalus* (Fieb.), pygofer and anal segment, left side ; B, pygofer, ventral view ; C, genital styles, ventral view ; D, basal suspensory sclerite of pygofer ; E, aedeagus, left side, apical membrane shown only in part. F, *Tettigometra sulphurea* Muls. and Rey, aedeagus and right genital style, shown in relation to pygofer ; G, pygofer, postero-ventral view. H, *Tettigometra virescens* (Panz.), anal segment, pygofer, and male genitalia seen by transparency, left side, with apical membranous sac of aedeagus omitted.

Phalix gen. n.

Head with eyes slightly wider than pronotum. Vertex between eyes 3·4 times as broad as long in middle, longer in middle than at inner margins of eyes, anterior margin broadly convex, posterior margin shallowly excavate, disc flat, slightly depressed basad of anterior margin, margins not carinate, a broad callus along apical margin between vertex and frons ; frons 2·2 times as broad at widest part as long in middle line, basal margin convex, lateral margins sinuately narrowed and carinate from near ocelli to fronto-clypeal suture ; disc smooth, ecarinate, slightly concave in profile ; clypeus about as long as frons in middle line, ecarinate, loral areas markedly produced laterad at base, rostrum rather longer than clypeus in middle line, surpassing mesocoxae but not nearly reaching post-coxae, apical joint longer than subapical ; antennae not surpassing exterior margin of eyes, second joint cylindrical, 4 times as long as broad and 3·3 times as long as first joint, ocelli facing anteriorly. Pronotum in middle line slightly longer than vertex, anteriorly shallowly convex, posteriorly very slightly concave, disc not depressed, smooth, ecarinate, mesonotum longer than vertex and pronotum combined, four-fifths as long as broad, disc smooth, shallowly convex; mesepimeral carina straight, diverging caudad from its counterpart on the opposite side; profemora 3·6 times as long as broad, not so long as to reach level of sides of body; post-tibiae 6 or 7-spined at apex, basal metatarsal joint with 7 spines at apex, second metatarsal joint with a spine on each side. Tegmina 3·3 times as long as broad, costal and sutural margins subparallel, apical margin asymmetrically and acutely curved, Sc + R simple, M forked at level of union of claval veins, posterior branch lying along Cu for a short distance then separating. Wings well developed. Seventh abdominal sternite of female posteriorly transverse; valvulae of ovipositor minute, subvaginal plate quadrate. Type species: *Phalix titan* sp. n.

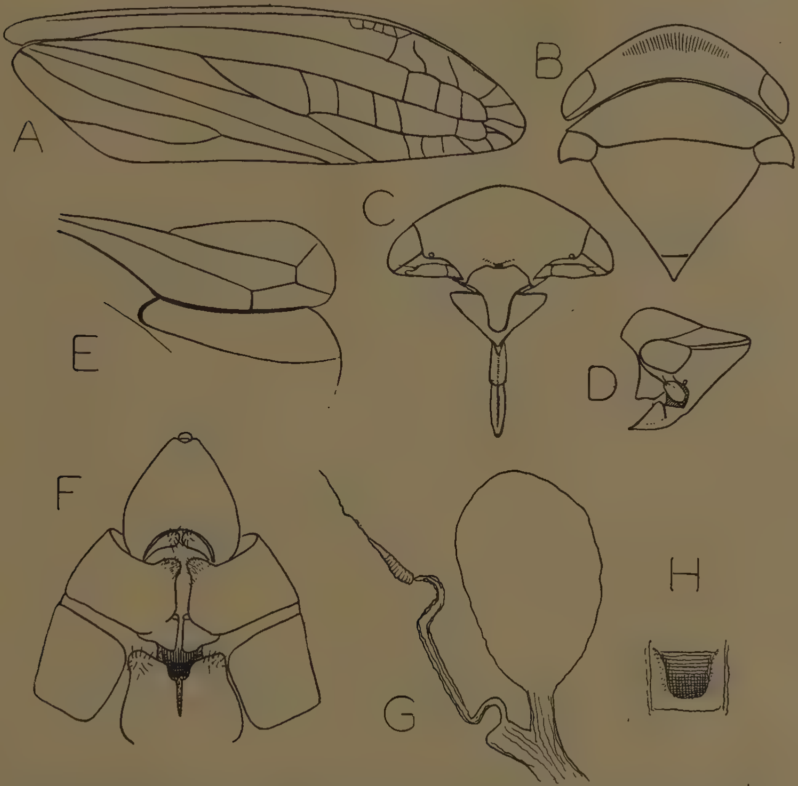

FIG. 3.—*Phalix titan* gen. et sp. n. A, tegmen; B, vertex, pro- and mesonotum; C, frons and clypeus; D, head in profile; E, anterior part of wing; F, female genitalia, ventral view; G, bursa copulatrix and spermatheca; H, subvaginal plate.

Phalix titan sp. n. (fig. 3, A–H).

Female : Length, 7·2 mm. ; tegmen, 7·0 mm.

Integument smooth, very finely and slightly rugose, not punctate. Tegmina lightly punctate, surface of a dull waxen appearance.

Bright yellowish-green ; a minute spot near middle of frontoclypeal suture, a band along basal margin of frons, third antennal joint, a minute spot at base of tegmen and another at apex of clavus piceous. Eyes red. Tegmina yellowish-green, costal margin narrowly creamy-yellow. Wings hyaline, powdered white.

Female genitalia as figured.

Holotype, ♀, UGANDA : Kawanda, 21.vi.1940 (*H. Hargreaves*).

This species is provisionally referred to Tettigometrinae in the absence of a male. It is readily distinguished from all other genera in the family by the shape of the head, and from all other Tettigometrinae by its relatively great size, it being the largest tettigometrid yet described.

Mesohilda gen. n.

Form generally similar to that of *Tettigometra* (*Tettigometra*). Vertex broader than long, apical margin angulately rounded ; disc of frons convex at base, becoming more weakly so near apex, and distinctly more vertical in apical half, as in *Hilda* ; rostrum surpassing mesotrochanters but not attaining post-trochanters ; apical joint longer than subapical. Post-tibiae laterally unarmed, apically 7 spined ; basal metatarsal joint with six or seven spines on distal margin, second metatarsal joint with two spines. Post-ocellar callus behind each eye tapering laterad, its posterior margin not parallel to posterior margin of eye.

Anal segment of male devoid of a tooth-like eminence on lower lateral margin. Aedeagus with stirrup-like basal suspension, distally in form of a sinuate simple tube of sub-equal width throughout, the latter passing into basal suspensory portion without interruption. Genital styles generally similar to those of *Tettigometra*, a boat-shaped sclerite between them and connected to them dorsobasally ; the sclerite continuing basad as a membranous sheath underlying the aedeagus. Type species : *Isthmia balteata* Distant.

Mesohilda balteata (Distant) (fig. 4, A–E).

Isthmia balteata Distant, 1907 : 201.

The figures are of the holotype.

Subfamily Hildinae.

Frons concave, distinctly or even strongly produced anteriorly at base ; apical joint of rostrum longer than subapical ; antennae more or less surpassing margin of eyes, not separated from them by a callus, second segment about four times as long as first. Profemora attaining or surpassing margin of closed tegmina ; protibiae exteriorly usually longitudinally sulcate throughout ; post-tibiae with seven or eight teeth at apical margin, basal metatarsal joint with seven teeth apically. Anal segment of male produced caudally into a long median upcurved process. Genital styles comprising an unpaired median plate with a lobe on each side near base.

Key to Genera of Hildinae.

(1) (2) Profemora not longer than width of head with eyes. Species usually less than 6 mm. total length including tegmina. Apex of vertex in dorsal view obtusely rounded ; frons usually with a velvety black band between ocelli and a broad pallid band distally . . . . **Hilda** Kirkaldy

(2) (1) Profemora longer than width of head with eyes. Species usually not less than 6 mm. total length including tegmina; apex of vertex in dorsal view strongly produced and acutely rounded or pointed; frons not as above . . . . (3)

(3) (4) Vertex anteriorly acute, almost pointed at apex; produced portion in profile slender, tapering distally, pointed or very sharply rounded at tip . . . . **Euphyonarthex** Schmidt

(4) (3) Vertex anteriorly more rounded, not nearly pointed at apex; produced portion in profile not slender, not or little tapering distally, rounded-truncate at tip . . **Raatzbrockmannia** Schmidt

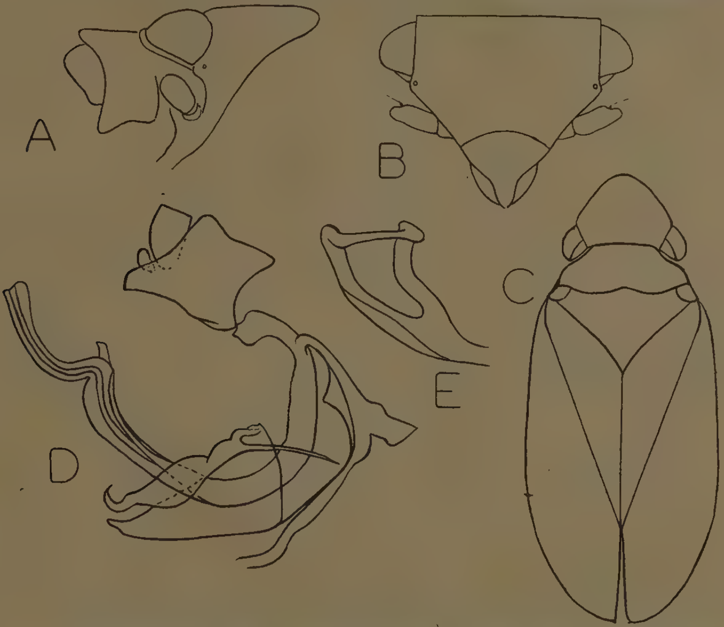

FIG. 4.—*Mesohilda balteata* (Dist.). A, head in profile; B, frons and clypeus; C, insect in dorsal view; D, anal segment, aedeagus and genital styles, right side; E, posterolateral view of basal part of aedeagus.

Hilda Kirkaldy.

Isthmia Walker, 1851 : 732 (*nec* Gray, 1821).
Hilda Kirkaldy, 1900 : 243. Orthotype, *Isthmia undata* Walker, 1851 : 732.
Nototettigometra Muir, 1924 : 219. Haplotype, *N. breddini* Muir, 1924 : 219.

It is not possible, on the basis of Muir's description and figures, to separate *Nototettigometra* from *Hilda*. The type locality of *N. beddini* is in doubt, and, as this species is extremely close to certain South African species (such as *Hilda patruelis* (Stål), the case in favour of its occurrence in South America (Peru) appears weak. Muir's comment that his genus " stands between *Tettigometra* Latreille and *Brachycephalus* Signoret (= *Brachyceps* Kirkaldy, n. n.) " would suggest that in 1924 he was not acquainted with *Hilda*. His earlier references to *Hilda breviceps* Stål (1923 : 221) refer, of course, to *Egropa*.

Hilda undata (Walker) (fig. 5, A–E).

Isthmia undata Walker, 1851 : 732.

The figures are from material in the British Museum (Natural History).

Euphyonarthex Schmidt.

Schmidt, 1912 : 461. Orthotype, *Euphyonarthex phyllostoma* Schmidt, *loc. cit.*
Tembandumba Distant, 1917 : 186. Haplotype, *Tembandumba buruana* Distant.

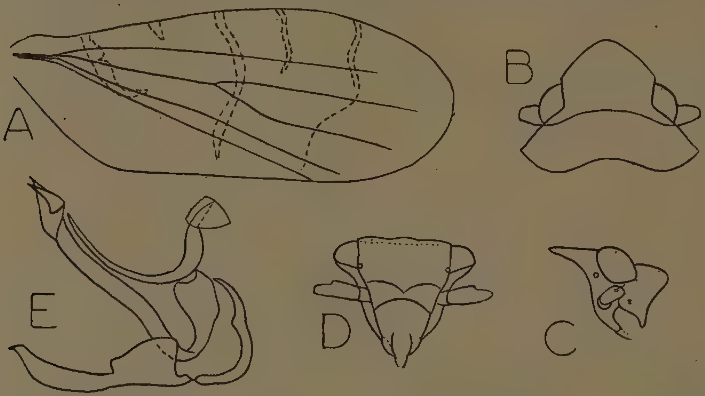

Fig. 5.—*Hilda undata* (Wlk.). A, tegmen; B, vertex and pronotum; C, head in profile; D, frons and clypeus; E, anal segment, aedeagus and fused genital styles, right side.

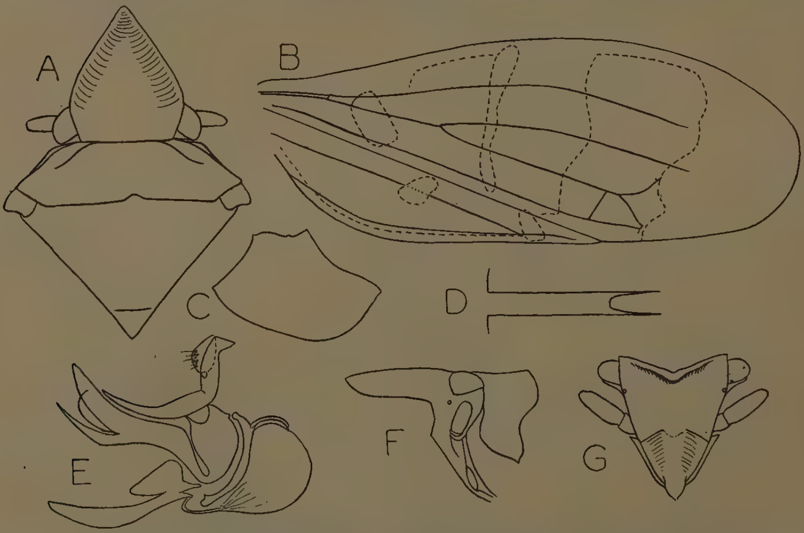

Fig. 6.—*Euphyonarthex buruana* (Dist.). A, head and thorax; B, tegmen; C, pygofer (not to same scale as preceding); D, medial cleft in posteroventral margin of pygofer; E, anal segment, aedeagus and fused genital styles; F, head in profile; G, frons and clypeus.

Euphyonarthex buruana (Distant) **comb. nov.** (fig. 6, A–G).

Tembandumba buruana Distant, 1917 : 186.

The figures are of Distant's type. The position of M fork is slightly variable, and may occur only one fifth from the base.

The series of *Euphyonarthex* in the British Museum comprises eight specimens of *E. buruana* Distant, fourteen of *E. phyllostoma ugandana* Lallemand and two unnamed. As it was collected in various localities it is possible that this material belongs to the single species *phyllostoma*.

Raatzbrockmannia Schmidt.

Schmidt, 1924 : 107. Orthotype, *Raatzbrockmannia inclinata* Schmidt.

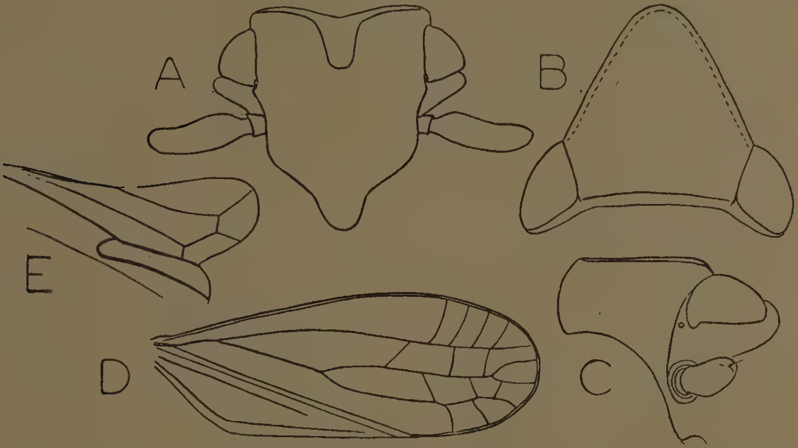

FIG. 7.—*Raatzbrockmannia inclinata* Schmidt. A, frons and clypeus ; B, vertex ; C, head in profile ; D, tegmen (on smaller scale than preceding) ; E, anterior part of wing.

Raatzbrockmannia inclinata Schmidt (fig. 7, A–E).

Schmidt, 1924 : 108.

The figures are of the female holotype.

This genus is closely allied to the preceding. *Raatzbrockmannia* is apparently known only from the type. In view of the considerable intrageneric plasticity of the tettigometrid head, the status of *Raatzbrockmannia* must for the present remain in doubt : *R. inclinata* may prove to belong to *Euphyonarthex*. The mesocoxae in these are relatively very short in comparison with *Tettigometra*.

Subfamily Egropinae.

Frons in profile not concave, produced at middle or medio-apically umbonate ; apical joint of rostrum longer than subapical ; antennae with second joint four times as long as basal joint, slightly surpassing eyes, and not separated from them by a callus. Profemora surpassing margin of closed wings ; post-tibiae with 6 or 7 spines at apical margin ; basal metatarsal joint with six or seven spines. Anal segment of male with lateroapical angles not prominent. Phallobase of aedeagus inflated, phallotreme situated in a small, laterally compressed distal lobe. Nymphs with head produced in a long curved process. Genital styles rod-like, distally recurved; between them a slightly sclerotised membranous plate deeply cleft medially on its posterior margin.

Key to Genera of Egropinae.

(1) (2) Frons not umbonate, strongly medially produced and carinate; in profile apex of vertex forming most anterior portion of head . . . . **Megaloplastinx** Schmidt

(2) (1) Frons umbonate near frontoclypeal suture, in profile frontal umbo, usually forming most anterior portion of head . . . . . . (3)

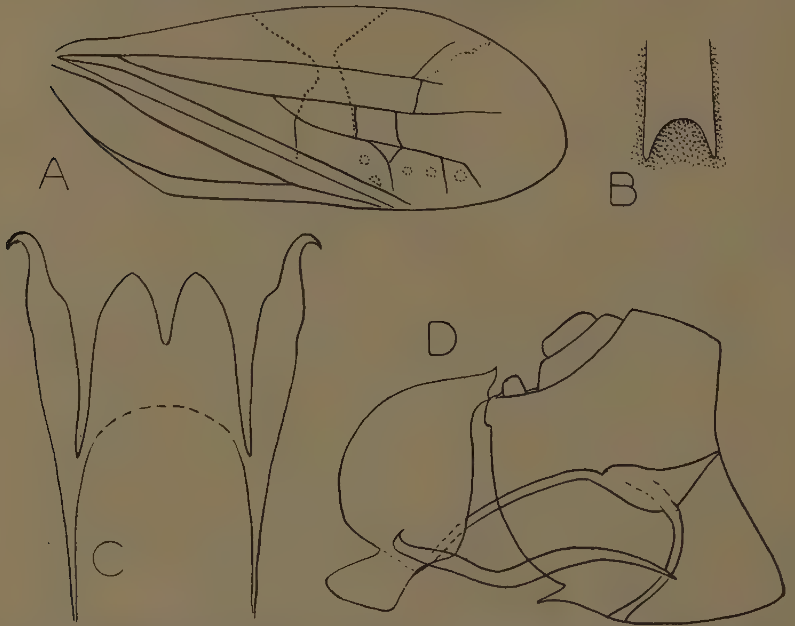

FIG. 8.—*Egropa malayensis* (Dist.). A, tegmen; B, base of cleft in posteroventral margin of pygofer; C, genital styles, ventral view; D, anal segment, pygofer and aedeagus, right side.

(3) (4) Vertex more than twice as broad as long in middle, anteriorly shallowly rounded; antennae little projecting beyond eyes; profemora shorter than width of head with eyes **Egropa** Melichar

(4) (3) Vertex less than twice as broad as long in middle, anteriorly obtusely angulate; antennae reaching far beyond eyes; profemora not shorter than width of head with eyes **Mesegropa** Baker

Egropa Melichar.

Melichar, 1903 : 82. Haplotype, *Egropa inusta* Melichar, 1903 : 82, pl. 3, figs. 13, *a*, *b*.

Egropa malayensis (Distant) (fig. 8, A–D).

Hilda malayensis Distant, 1909 : 41.

The figures are of the type.

The species of *Egropa* are comparatively uniform. The frontal eminence is a little variable within species, and slightly more so between them. Baker's figure of the head of *E. malayensis* (Distant) does not appear quite correct : in the holotype the anterior and posterior margins are almost parallel, and the vertex is only in the slightest degree longer in the middle than at the sides. The holotype of *E. tenasserimensis* Distant is a female. The statement by Baker that several dark subquadrate spots (sometimes with white centres) near the apex of the clavus are developed only in males does not hold good : they are, for instance, fully developed in the female type of *E. malayensis* Distant.

Mesegropa Baker.

Baker, 1924 : 98. Orthotype, *Mesegropa sumatrensis* Baker.

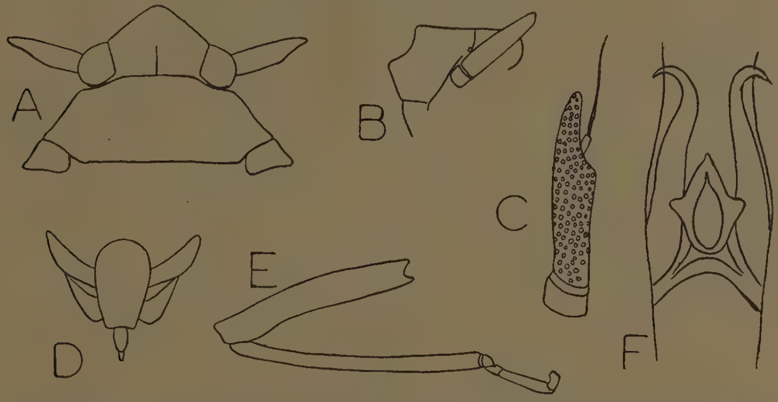

Fig. 9.—*Mesegropa sumatrensis* Baker. A, vertex and pronotum ; B, head in profile ; C, antenna ; D, clypeal region, anterior view ; E, leg ; F, male genital styles, ventral view. (All figures after Baker.)

Mesegropa sumatrensis Baker (fig. 9, A–F).

Baker, 1924 : 99.

The figures are redrawn from Baker. This collection by Corporaal, still apparently unique, is most fortunate, as it throws light on the steps by which the transition from *Egropa* to *Megaloplastinx* has been achieved. As *Megaloplastinx*, *Mesegropa* and the hildine genera *Euphyonarthex* and *Raatzbrockmannia* are all of very large bodily size for Tettigometridae, it might appear that the extraordinarily disproportionate elongation of the legs and the upward carriage of the eyes has resulted simply from allometric growth. Such a possibility, however, is heavily discounted by the fact that *Phalix*, larger than them all, is of normal tettigometrid proportions. In *Mesegropa* elongation of the legs has not proceeded quite so far as in *Megaloplastinx*, while the head is unmodified from the condition found in *Egropa*.

Megaloplastinx Schmidt.

Schmidt, 1912 : 459. Orthotype, *Megaloplastinx carinifrons* Schmidt.

Megaloplastinx carinifrons Schmidt (fig. 10, A–F).

Schmidt, 1912 : 461, fig. 1.

The figures are of a specimen in the British Museum.

In this genus the ocelli are separated from the disc of the frons by the lateral marginal carinae. According to Muir (1924 : 22) the frons of the nymph is drawn out into a long process, as in other Egropinae. It is evident, from the general facies of the insect, that *Megaloplastinx* has evolved, in Egropinae, in an exactly parallel manner to *Euphyonarthex* and *Raatzbrockmannia* in Hildinae. If the profile of the latter genus is superimposed with a slight downward tilt on that of *Mesegropa*, with its characteristically egropine mediodistal frontal eminence, it will be seen that the conjugate profile so produced is closely comparable to that of *Megaloplastinx*. It is indeed not unreasonable to suppose that the shape of the head in this genus is determined by two different sets of growth factors—the fundamental egropine set of growth-determinants plus a further set of incursive " euphyonarthecoid " mutations.

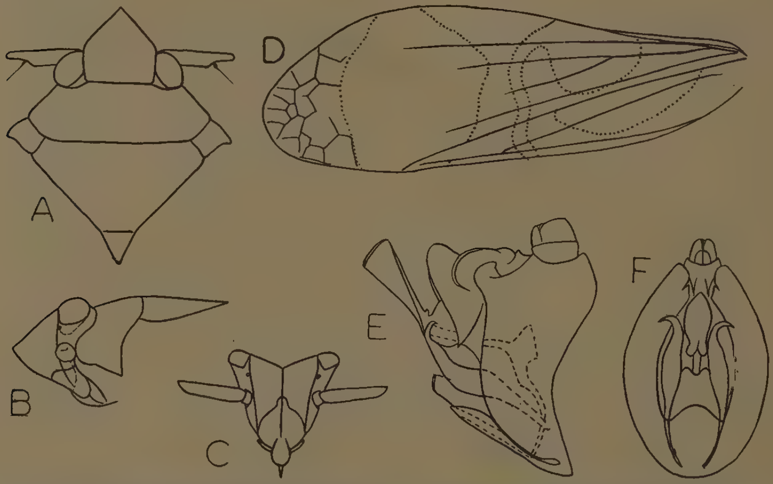

Fig. 10.—*Megaloplastinx carinifrons* Schmidt. A, vertex, pronotum and mesonotum ; B, head in profile ; C, frons and clypeus ; D, tegmen ; E, anal segment, pygofer and male genitalia, right side ; F, ditto, posteroventral view. (E and F after Muir).

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THE *CHARAXES ETHEOCLES-ETHALION* COMPLEX: A TENTATIVE RECLASSIFICATION OF THE GROUP (LEPIDOPTERA: NYMPHALIDAE).

By V. G. L. van Someren, F.R.E.S.,

and

T. H. E. Jackson, F.R.E.S.

Manuscript received 19th October, 1951.

(Read 7th May, 1952.)

Introduction.

The *Charaxes etheocles-ethalion* complex has been a puzzle to students of African Lepidoptera for more than half a century, and although *Charaxes ethalion* Boisduval has been recognised as distinct from *Charaxes etheocles* Cramer for many years, the females of the two species are still confused and many distinct species are still united under the name "*etheocles*" in all current publications.

The confusing similarity of the species suggests that they are of recent origin, and that the ancestral "*etheocles*" had an extensive range, possibly in an east to west direction. Owing to the very considerable geographic changes which took place from time to time in the northern and central areas of the continent of Africa, a splitting up of the species may have occurred; the residual groups which survived may have become modified as the result of changed ecological conditions. With a gradual settlement and development of more suitable environment, these modified residual forms may have spread and come together and even overlapped.

Temporary (in terms of geological time) isolation may have given rise to changes in the gene complex and physiological changes may have taken place as a result of adaptation to changed environment and, possibly, adoption of a different food-plant. This might give rise to a sufficient degree of isolation to deter or even prevent crossing, resulting in further stabilisation of the form, until it became what we now term a "species." Further modification may have taken place in certain areas which gave rise to mimetic patterns such as we note in the female forms *manica* Trimen, *cedreatis* Hewitson, *rosea* Butler, etc.

The first comprehensive review of the group was undertaken by Rothschild and Jordan (1898–1900, *Novit. Zool.* **5**–**7**). The authors made a thorough search of the literature and examined many types; they made numerous genitalia dissections. They came to the conclusion that there was little significant difference in the male genitalia of all specimens examined with the exception of *Charaxes ethalion* Boisduval, which was sufficiently distinct to be readily recognisable. This placed *ethalion* males apart from the rest, but it did not clear up the difficulty of some female forms which resembled to a marked degree females of "*etheocles*." In this review four male and several female "forms" were described, and *Charaxes viola* Butler was placed as a subspecies of "*etheocles*." Without evidence of bred material, "*etheocles*" was left as a species highly variable in both sexes.

The next general account was by Aurivillius (1911, *in* Seitz, *Macrolepidoptera of the World*, **13** (*African Rhopalocera*): 135-137). This author followed the grouping sponsored by Rothschild and Jordan, dealing with the males separately from the females, and maintained that no male could be definitely associated with a given female with certainty until breeding experiments had been carried out. The "*etheocles*" group was treated as one variable species, and this policy has been followed by all authors up to date.

During 1923–24 a limited number of breeding experiments were undertaken by Dr. R. A. L. van Someren at Jinja, Uganda, at the request of the late Professor Sir Edward Poulton of Oxford. The results were submitted to Sir Edward, who communicated them to the International Entomological Congress, Zurich, in July, 1925. These bred "families" seemed to support, to some extent, the conception that in the Jinja area three female forms, viz., *vansomereni* Poulton, *cedreatis* Hewitson and *carpenteri* Poulton, were associated with the male *picta* Rothschild. Shortly afterwards, though not in time to correct the error, it was discovered that the African who attended to the feeding of the larvae had inserted wild caught larvae with their respective food-plants to maintain the number of larvae and make good losses due to deaths! The experiments were thus unreliable and misleading.

A further series of experiments was undertaken in 1928–30, also in the Jinja area, but carried out under strict supervision; additional breeding was done in the East Elgon area also. These results indicated where, and to what extent, the first experiments were misleading.

In 1932 van Someren and Rogers dealt with the East African representatives of the "*etheocles*-complex" (1932, *J. E. Afr. Ug. nat. Hist. Soc.* **42–43** : 141–172), and submitted evidence, as a result of these further breeding experiments, that the complex consisted of several distinct, though, in the male, remarkably similar species. Thus, on page 240, "from the evidence of this bred material we are able to suggest: (*a*) that there is certainly one main species with geographical representatives (races) in Kenya and Uganda; (*b*) that there are two or more females with their respective males which are distinct from this species and from each other." No attempt, however, was made to revise the classification, and the nomenclature used followed that given in Rothschild's Monograph, supplemented by identification of specimens submitted to Dr. Jordan.

Since 1932, much additional evidence has been accumulated by breeding and by extensive collecting, combined with close observation regarding distribution and food preference. As a result of these additional data we drew up a revised classification and, in May, 1950, one of us (Jackson) took the opportunity of a brief visit to England to check this grouping with the extensive material in the British Museum (Natural History) at South Kensington and at

Tring, and in the Hope Department of the Oxford University Museum. Although this re-grouping was essentially correct within the limits of its purview, it became evident that in order to obtain a true picture of the "*etheocles*-complex" the whole group would have to be studied on a pan-African basis.

Through the kindness of the authorities concerned all available material was studied, and at the invitation of the Keeper of the Entomological Department of the British Museum (Natural History), all the material in the Rothschild and other collections in the Museum was amalgamated in a general rearrangement of the group. This comprehensive view of the group gave an insight into the distribution of the various "forms" and a critical examination of the underside coloration and pattern (important in other sections of Nymphalidae), enabled us to associate male and female with a fair degree of certainty. It was found that most species can be easily separated by good morphological characters, even in the males, or are at least separable in series. In many instances supporting evidence was furnished by knowledge of larvae and food-plants and bred families. The resultant re-grouping presented some semblance of a natural classification. It entailed the recognition of several distinct species, some with well-defined races, and the re-allocation of named males and females. Certain sexes appeared to be undescribed, and this omission is made good in the text which follows.

Although the International Rules of Zoological Nomenclature take no cognisance of names lower than subspecific, we follow the usual procedure of recognising form names already applied and utilising them for species and geographical races as the case may be. We are given to understand that the new Rules recommended by the International Commission provide for this procedure.

We wish to emphasise that the re-grouping we submit is incomplete in many details, especially in regard to West and South African material, and much more breeding will have to be done before our knowledge of some species is fully complete ; thus this paper must be taken as an interim report.

The classification which follows gives a more correct view of the "complex" than has been possible in the past, and we hope that it will stimulate interest in the problem and induce others to supply further data based, if possible, on breeding from known parents.

No re-examination of the genitalia has been carried out, since most, if not all, of the species and races here mentioned were carefully compared by Dr. Jordan, and no constant difference was noted in any save *Charaxes ethalion*.

For brevity's sake we have not included full references to the previous literature on the species dealt with in this paper. Only such necessary references as are not to be found in Aurivillius and Rothschild and Jordan (*see above*) are given.

ACKNOWLEDGMENTS.

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SYSTEMATIC CLASSIFICATION.

Charaxes ethalion Boisduval, 1847.

The following forms are discussed below :

♂♀ *ethalion* Boisduval, 1847, type loc. Natal.
♂ f. *kitungulensis* Strand, 1911, type loc. Kitungulu, German East Africa.
♂ f. *rosae* Butler, 1895, type loc. Natal.
syn. f. *rosa* van Someren, *op. cit.*, type loc. Rabai, Kenya.
♀ f. *swynnertoni* Poulton, 1918, type loc. Rhodesia.
♀ f. *ethalionoides* Hale Carpenter, 1943, type loc. Rabai, Kenya.
♀ f. **howardi** f.n., type loc. Chepalungu, Sotik area, Kenya.

Description and Taxonomy.

No racial forms have been described, but one or more may have to be admitted. Thus, for example, the only female form (taken in numbers) from the Mt. Marsabit area is a large insect of distinctive characters, resembling but not identical with *swynnertoni* Poulton, and, furthermore, Mr. B. D. Barnes informs us (*in litt.*) that there are high and low veldt forms in Rhodesia which constantly differ from each other. It is also significant that the yellow marked form of female form *ethalion* does not seem to occur in the Kenya Highlands.

The male of this species has been accepted as distinct from *Ch. etheocles* auct. for many years.

The genitalia are distinctive. Wings comparatively short and relatively broad, an impression enhanced by the almost straight outer margin to *f.w.*. Colour velvety-black without metallic sheen ; blue spots reduced or obsolete ; *f.w.* with almost continuous white fringe. *Uns.:* earth-brown or with a vinaceous tinge, almost uniform in colour, and dark lines narrow and often indistinct.

♂ f. *kitungulensis* Strand.—None examined from type locality, but description agrees with a common variant of male found throughout the range of the species.

♀ f. *ethalion* Boisduval.—Discal bar and spots on *f.w.* white or pale bluish ; a spot often present in the cell. *H.w.* bar white or shaded with blue. An equally common form has *f.w.* spots yellowish to ochre-orange.

♀ f. *ethalionoides* Hale Carpenter.—Originally described as a form of *Ch. etheocles* Cramer. Hardly differs on upper side from nominotypical form, but discal spots reduced and post-discal spots obsolete in 1a–3. Has been bred in families with *ethalion* males and *rosae* females, and hardly deserves recognition.

♀ f. *rosae* Butler.—Originally referred to *Ch. etheocles*. Type examined and undoubtedly belongs to *ethalion*. *F.w.* discal bar curved to apex of cell and costa, white to bluish white ; *h.w.* bar white shaded with blue, extending through to costa or stopping short in area 7.

♀ f. **howardi** f.n.—Similar in pattern to *rosae*, but all light areas orange tawny ; *h.w.* bar slightly paler toward inner margin.

Holotype ♀, KENYA : Chepalungu Forest, 1.x.1949 (*H. D. van Someren* leg.) in Coll. van Someren.

♀ f. *swynnertoni* Poulton.—Similar in pattern to nominotypical form, but all light areas strongly blue.

It should be noted that in all female forms of this species the post-discal series of spots on the fore wing is strongly angled or inclined towards the costa in areas 5–7. There is often a blue spot towards the apex of the cell in the fore wing above, and this character is not diagnostic of *Ch. etheocles* sens. lat., as is often thought.

Breeding.

The species has been bred at the Kenya coast on *Parkia fillicoidea* (Leguminosae), a female *ethalion* producing female forms *ethalion*, *ethalionoides* and *rosae*. In the Kenya Highlands it has been bred on *Scutia indica*, *Scutia buxifolia* (Rhamnaceae), *Albizzia sassa* (Leguminosae) and *Gymnosporia* sp. (Celastraceae). It lays on *Albizzia* sp. in Natal and Rhodesia. In the Hope Department, Oxford, a family from Rhodesia produced female *swynnertoni* and one yellow-marked female *ethalion* ; another only *swynnertoni*.

Mimetic Associations.

In Eastern Africa *Ch. ethalion* flies with *Ch. catachrous contrarius* Weymer, *Ch. aubyni* Poulton, *Ch. pembanus* Jordan, and meets subspecies of *Ch. viola* Butler on the edges of forests. Female form *rosae* is the model for *Ch. catachrous contrarius* ♀ f. **pseudorosae** f.n. (see p. 279), and of the female of *Ch. pembanus* Female form *ethalion* is the model for the other female form of *Ch. c. contrarius*, while its own models are *Ch. brutus* Cramer (both sexes) and the females of *Ch. cithaeron* Felder and *Ch. violetta* Grose Smith. The model of the *swynnertoni* form is *Ch. cithaeron*.

Habitat and Distribution.

Ch. ethalion is primarily a forest insect, although it may be noted occasionally in the open savannah country. It is an eastern and southern species, occurring in Kenya (east Rift), through Tanganyika Territory, Nyasaland, Portuguese East Africa to Rhodesia and Natal. It has been taken occasionally in western Kenya, Kisii-Suna area, along with *Ch. viola phaeus* Hewitson, and also in the Chepalungu forest of Sotik area. Specimens were also taken in the Jinja area of Uganda in 1922–1931, but the species has not been recorded since from this locality.

Details of the distribution and characteristics of the female forms, as shown by material in the British Museum and in the authors' collections, are as follows :

Cape to Natal : ♀ f. *ethalion* with fore wing bar and spots tinged yellowish buff. Spots tend to be reduced in size in fore wing, but hind wing band broad. No other forms recorded from here.

Rhodesias : ♀ f. *ethalion* with fore wing spots white or yellowish or ochreous ; the forms *rosae* and *swynnertoni* also occur. Through the kindness of Mr. B. D. Barnes we have been able to examine the following additional material : One male, Vumba Mts., one female, Vumba Mts., one female, Gwanda, S. Rhodesia. These specimens present the characteristics of *ethalion*, the females being yellow to tawny-ochre spotted in fore wing. The female from Gwanda is small and lacks the white median band below—a not unusual variation. One of the Vumba females has been recorded as *Ch. etheocles* f. *kirki* Butler (Pinhey, 1949, *Occ. Pap. nat. Mus. S. Rhod.* **2** : 15), but an examination of this specimen shows it to be an orange marked female of *ethalion*.

Nyasaland : ♀ f. *ethalion* with fore wing spots and bar white or yellowish. In some of the yellow marked specimens from here the discal and subapical spots are joined by yellowish scales to form rays. They run slightly larger. Forms *rosae* and *swynnertoni* are also present.

PORTUGUESE EAST AFRICA : ♀ f. *ethalion* white or yellow marked; also *swynnertoni* and *rosae.*

ANGOLA : Three males only.

TANGANYIKA TERRITORY : ♀ f. *ethalion, rosae* and *swynnertoni.*

KENYA COLONY : Coast to Kibwezi and east Rift : ♀ f. *ethalion*, mostly, if not all, white-spotted in fore wing; size of spots variable; form *rosae* occurs commonly at the coast, but *swynnertoni* is absent. ♀ f. *swynnertoni* occurs in the Nairobi area together with *rosae.* The only form from Mt. Marsabit is a large bold form like *swynnertoni.* In South Kavirondo and Chepalungu forms *ethalion* and *howardi* occur.

UGANDA : Six males in Coll. van Someren taken 1922–1931 in Jinja area.

Charaxes viola Butler, 1865.

Butler's *Charaxes viola* was based on a female from "West Africa" (the type locality) described in 1865. The same author subsequently described the male quite correctly in 1876.

The species has a very wide range from west to east and south, inhabiting the savannah country of diverse elevation, and it is therefore not surprising to find that it splits up into several recognisable races. Some of these now show signs of spreading to the adjoining territory of another race. The degree of isolation each has acquired is a matter for close study in the field; the subject is important and intriguing and well worth further investigation.

Seven subspecies are recognised.

(i) *Charaxes viola viola* Butler, 1865.

Description and Taxonomy.

Male : Size small, length *f.w.* 30–33 mm., pointed and somewhat falcate. *Ups.:* Ground-colour black, a prominent blue spot in cell towards apex, a large whitish spot in cellule 6, two conspicuous white post-discal spots in 6–7, outer margin strongly and widely glaucous greyish green interrupted by black veins. *H.w.* black with submarginal row of bluish-white streaks; an undulating post-discal line of greenish from above upper tail, then greenish to anal angle. Compared with subsp. *picta* Rothschild, males more heavily spotted. *Uns. :* Clayish ecru-drab, rather uniform in colour; median interspaces scarcely darker than base; dark line narrow but distinct.

Female : Ups.: Ground colour purplish-brown; *f.w.* with a series of discal and post-discal orange spots conjoined in 1*a*–3 or 4, then as separate spots or thinly connected by tawny scales; outer margin with subdued tawny interrupted by dark veins; a series of submarginal white or bluish streaks; margins above tail tawny-red then greenish to anal angle. *F.w.* and *h.w.* bands broad. *Uns.:* Ecru-drab. *F.w.* discal and post-discal interspaces creamy-buff to straw colour, distal halves dark cinnamon rufous. Compared with subsp. *picta* female (= *vansomereni* Poulton) wing bands are broader and paler and *h.w.* band more violet tinged.

Ch. viola was placed as a subspecies of *etheocles* by Rothschild and Jordan (*op. cit.*).

Breeding.

There are no published records of *viola* having been bred, but the fresh condition of a series in the British Museum suggests that it may have been.

Mimetic Associations.

There appears to be no direct model for this species or of any of its subspecies, but Sir Edward Poulton (1925, *Verh.* **3** *Int. Kongr. Ent.*) suggests that *Ch. epijasius* Reiche may be the influencing agent in West Africa to Kavirondo; this cannot apply to Kenya and its coast belt.

Habitat and Distribution.

This subspecies occurs in the open upland areas of Nigeria to Lake Chad. There is a long series in the British Museum from Nigeria, Gambia and French West Africa. The type female from "West Africa" (no other data) bears a note below which states "*Ch. chiron* Staud.: agrees with figure, 1909."

(ii) *Charaxes viola picta* Rothschild, 1900.

Charaxes viola picta Rothschild, 1900, type loc. Unyoro, Uganda.
♀. Poulton, 1925 (*as vansomereni*), type loc. Buyala, Uganda.

Description and Taxonomy.

Male: Very similar to male *viola viola* Butler. *F.w.* blue spot in cell always present; one large and one small whitish discal spot below costa, two subapical post-discal spots white, and these may be followed by a series of greenish spots to hind angle; marginal lunules broadly greenish-grey. *H.w.* as in nominotypical race; post-discal wavy greenish line usually present up to veins 3–4. Wings pointed, falcate.

Female (= *vansomereni* Poulton): Very similar to typical female *viola* but *f.w.* bar usually narrower; *h.w.* band white with bluish tinge, narrower than in nominotypical race. *F.w.* orange bar may shade to white in 1a–1b; discal and post-discal orange spots may be fused up to 5, or post-discal spots may be discrete from 4–7. An orange spot may or may not be present in the cell; marginal lunules tawny-cinnamon and this colour may suffuse entire outer portion of wing up to bar. *H.w.* bluish-white band may be suffused with orange in 5–6 to costa (a mutant toward the form *kirki* in *viola kirki* Butler).

The male ascribed to *kirki* by Butler, from Foda, near Wadelai, Albert Nile (Emin Pasha), is certainly *picta* Rothschild. Rousseau-Decelle (1938, *Bull. Soc. ent. Fr.* **43**) described two female forms of *Ch. etheocles* under the names *illuminata* and *splendens*. From the descriptions these appear to be merely variations of the female of *Ch. viola picta*. Both came from the Belgian Congo.

Breeding.

Several families have been bred from known parents in the Jinja area, Uganda. The larval food-plants are *Albizzia coriaria* (Luganda: Mugavu), *Entada abyssinica* and *Entada* sp. (Luganda: Mworora) (Leguminosae). Males are always *picta*, females always *vansomereni*. Many other families were bred in the East Elgon area, Kitale, in 1931–1932, where the food-plants are *Entada abyssinica* and *Albizzia gummifera*. These families also gave male *picta* and female *vansomereni* only.

The horns on the larval heads are long, tapering, straight or slightly incurved at tip; uniformly green or red-tipped.

Habitat and Distribution.

The subspecies is found in open savannah woodland (orchard country) in areas where the food-plants are present. It may occur at the fringe of forest where *Albizzia* is growing near swampy ground, and thus also along riverine fringing forest. The range appears to be North-western Kenya Colony: lower Sotik, Chepalungu, S. Kavirondo (where it meets *viola phaeus*), Central and N. Kavirondo to Nandi and Elgon, then through Uganda and part of Karamoja (where it meets *viola suk* Hale Carpenter and Jackson) to S. Sudan and the eastern Congo. It apparently extends to the Cameroons (one female in the British Museum), and there are six males (Levick Bequest) labelled 'Togoland.'

(iii) *Charaxes viola daria* Rothschild, 1900.

♀. *Charaxes viola daria* Rothschild, 1900, type loc. Jabalo Gugura, Abyssinia.
♂. See below.

Description and Taxonomy.

Male: This sex of this subspecies has not been described. Very similar to male of *viola kirki*, but larger. Wings pointed, falcate. *Ups.: F.w.* black with greenish sheen; two subapical yellowish spots, one post-discal spot with a minute dot below it; a bluish spot at end of cell; marginal lunules greyish-green. *H.w.* tails short; a row of small submarginal greenish spots becoming bluish at anal angle; marginal lunules reddish above upper tail, greenish to anal angle. *Uns.:* Similar in pattern to other races of *viola* but ground-colour dark chocolate brown.

Neallotype ♂ ABYSSINIA: Adola, vi.1942 (*M. S. Berkeley* leg.) in British Museum (Natural History).

Female: Pattern as in female of *viola picta* but *f.w.* discal bar and spots white to cream; *h.w.* band creamy-white to white.

There is an interesting female in the Paris Museum, taken in Abyssinia, in which the pattern is as described above, but the bands on both wings are creamy yellow. This may be the 'female form near *vansomereni* Poulton,' recorded by Ungemach and quoted by Carpenter (1935, *Trans. R. ent. Soc. Lond.* **83**).

Breeding.

There are no records.

Habitat and Distribution.

There is a long series of males from many parts of Abyssinia in the British Museum; also three females from Jabalo Gugura (type 1900, Gillet Mts. 1900 (*Neumann*), and 10 miles north of Miessa, 1946 (*Guichard*). The authors' collections contain a few males from Adola and Gimma, Abyssinia.

(iv) *Charaxes viola kirki* Butler, 1881.

The following forms are known:

♀ f. *kirki* Butler, 1881, type loc. Mamboia, Tanganyika Territory.
♀ f. *albifascia* Poulton, 1925, type loc. Dabida Mt., Kenya Colony.
♀ f. *rogersi* Poulton, 1918, type loc. Dabida Mt., Kenya Colony.
♀ f. *daria* Rothschild, 1903, type loc. 'between Jabalo and Gugura,' Abyssinia.
  syn. f. *handari* Poulton, 1925, type loc. Handari, near Mvumi, Tanganyika Territory, **syn. n.**

Description and Taxonomy.

As already mentioned under *Ch. viola picta*, the male ascribed to *kirki* by Butler which came from Foda, Wadelai (Enim Pasha), is *picta* Rothschild. The second male cited, but not described, by Butler (1891, *Ann. Mag. nat. Hist.* (4) **7** : 42) as *kirki* came from Kandera, Tanganyika Territory, and rightly belongs here. This specimen, however, cannot be considered as the neallotype male as the citation is unaccompanied by any description. The male therefore appears to be undescribed.

Male : Ups.: Black with slight greenish sheen. *F.w.* with two yellowish to ochreous subapical spots, a large yellowish post-discal spot with a dot below it, a bluish spot in the cell toward the apex ; marginal lunules greenish-grey. *H.w.* marginal lunate spots green from anal angle to vein 2, then reddish to area 5 ; a row of bluish-white submarginal dots beyond these a greenish wavy line, sometimes obsolete. *Uns.:* Ground-colour smoky-grey brown, black lines and spots fine but heavier at base and hind portion of *f.w.* ; post-discal row of yellow and red lunate spots usually well marked.

Neallotype ♂, Kenya Coast : Kilifi, iv.1943 (*T. H. E. Jackson* leg.) in British Museum (Natural History).

Female : Ups.: Ground-colour blackish-brown ; *f.w.* with orange bar formed by a series of discal and post-discal spots fused from hind margin to 6, then spots discrete or only slightly conjoined by tawny scales, but always free below costa ; an orange spot usually present in the cell toward apex. *H.w.* band white or bluish tinged with some tawny orange suffusion in upper portion.

♀ f. *albifascia* Poulton.—Similar to *kirki*, but *h.w.* band white, bluish tinged, and without tawny suffusion. Compared with female of *viola picta* (= *vansomereni*) *h.w.* band narrower and less shaded with blue.

♀ f. *rogersi* Poulton.—Very similar to *kirki*, but *h.w.* band strongly suffused with, or entirely, tawny-orange.

♀ f. *daria* Rothschild (= *handari* Poulton).—Pattern as in *kirki* but *f.w.* and *h.w.* bars white to creamy-white.

In the description of *handari* (1925, *Verh.* **3** *Int. Kongr. Ent.*) Poulton states that the type was compared with the type of *daria* by Dr. Jordan, and mentions certain differences ; but a re-examination of these types, together with additional material, indicates that the slight differences are individual. This remark applies equally to *achaemenesopsis* Hale Carpenter and Jackson ; it is the *daria* form in another race. It should be noted, however, that this form is a rare variant amongst females of *viola kirki* ; it is a dominant stable form in *viola* f. *daria* and in *viola suk.*

Breeding.

There are no records of bred material from Tanganyika Territory. In the Kenya coastal belt this race has been bred on *Albizzia sassa* ; in the Voi-Kibwezi area on *Albizzia* sp. and *Entada* sp. in the Nairobi area on *Albizzia sassa.* From eggs laid by known females only one type of male, viz. *kirki*, has been produced, together with female forms *kirki* and *albifascia* and transitions towards *rogersi.*

Habitat and Distribution.

This race inhabits the savannah bush and orchard country, forest fringes and riverine forest. It is not infrequently taken in open areas of forest, for here *Albizzia* grows around the black cotton areas of low land. Its range would seem to be through east central Tanganyika to the Kenya coast, and through the hinterland to Voi-Kibwezi and Teita, and to the high ground around Nairobi-Kikuyu, east of the Rift, but not to the Meru-Jombeni areas north-east of Mt. Kenya. In the low Masai country and in Ukamba a smaller bio-ecological strain occurs which shows a marked tendency toward *Ch. viola suk* and it is known that these breed on *Acacia mellifera* as does *viola suk*, and not on *Albizzia*. (For further remarks *vide* p. 267 under *Ch. viola suk*).

Material Examined.

The female type of *kirki* from Mamboia, Tanganyika Territory, which is in the British Museum, together with a series of both sexes from the Kenya Coast, including females *kirki*, *rogersi* and *albifascia* ; from East-central Tanganyika Territory with *kirki* females ; from Kibwezi males with female *kirki*, *albifascia*, and one female form *daria*. In the Hope Department, Oxford, there is one female of form *daria*, i.e., the type of *handari* Poulton. In the authors' collections material from Handeni and Mkomasi, Tanganyika Territory ; males and females from the Kenya Coast to Voi-Bura-Teita, Kibwezi, Ukambani and Nairobi, the females being *kirki*, *albifascia* and transitions toward *rogersi*. No full *rogersi* seem to occur in the Kenya Highlands.

(v) *Charaxes viola suk* Hale Carpenter and Jackson, 1950.

The following names apply :

♂, ♀ types (as *Ch. etheocles suk*) Hale Carpenter and Jackson, 1950, type loc. Kacheliba, Suk, Uganda.
♀ f. *kirki* Butler, 1881, type loc. Mamboia, Tanganyika Territory.
    syn. f. *kirkoides* Hale Carpenter and Jackson, 1950, **syn. n.**
♀ f. *albifascia* Poulton, 1925, type loc. Dabida Mt., Kenya Colony.
♀ f. *daria* Rothschild
    syn. ♀ f. *achaemenesopsis* Hale Carpenter and Jackson.
♀ f. *intermedia* Hale Carpenter and Jackson, 1950, type loc. Kacheliba, Suk, Uganda.

Description and Taxonomy.

Although this subspecies was described so recently, it is advisable to state the chief features of difference between it and the subspecies *kirki*.

Male : In size it is small; on a general average smaller than *kirki*, *chanleri* or *picta*. Wings more pointed and more falcate, but some small *kirki* may approach them in this respect. *Ups.:* Markings as in *kirki*, but subapical spots less ochreous, and may be bluish ; subcostal spots may be bluish or the upper one white ; spot toward apex of cell blue ; marginal glaucous greyish-green lunules less wide. *Uns.:* Ground-colour cold greyish, less brownish than in *kirki*, a point emphasised in a long series.

Female : All female forms described in the original paper and designated by new names are already named forms, with the exception of *intermedia*, which is transitional between *daria* and *albifascia*. These forms in subspecies *suk* differ only by their smaller size and greyer underside.

Breeding.

No families have been raised from known parents, but the females lay on *Acacia mellifera* (Mimosacae). Odd specimens have been bred on this food-plant in the lower Masai and Ukamba country and in form and size they are transitional to *viola suk.*

Habitat and Distribution.

This subspecies inhabits the dry thorn bush country where *Acacia mellifera* is one of the dominants. It ranges from the Karamoja-Suk country, from which a very long series has been taken, then apparently occurs again in transitional form in the Ukamba-Masai country, where this food-plant is again one of the dominants. It meets with *Ch. viola picta* in the Karamoja country ; it meets and overlaps *viola kirki* in South Ukamba and eastern Masai, the overlap being particularly noticeable in the Kibwezi area. Material in the British Museum, placed to *viola kirki*, suggests the possibility that large and small males are seasonal, the larger appearing in January to June, and the smaller from July to September, but material in our collections shows that this does not hold good. Thus in Coll. van Someren there are large specimens from Kibwezi taken in March, May, October and December, and smaller examples in January, March and July. It should be noted that in the Kibwezi area *Albizzia* occurs in the riverine fringing forests and *Entada* on the higher ground (as in Karamoja, thus providing food for *Ch. viola picta*), whilst *Acacia mellifera* is widespread in the thorn bush.

Intermediates have not been taken in the areas of overlap or contact, and this may be accounted for by the degree of isolation derived from food preference.

In this tentative regrouping of *Charaxes viola* we are influenced in our decision to maintain *suk* as a subspecies distinct from *kirki* by two main reasons : (1) The fact that in Suk and Karamoja the female form *daria* occurs in more than a fifty-fifty proportion with other forms, whereas it is a rare variant in the subsp. *kirki*. In the original series taken in Suk the proportions were 16 *daria*, 8 *kirki-albifascia*, 2 *intermedia*, and further collecting confirms this preponderance of the white-banded form. In contrast, in a very long series of *kirki* females (nearly one hundred), only two *daria*-like females, one from Handari and one from Kibwezi, have been noted. This indicates very emphatically that there is a distinct gene difference in the two races. (2) The importance of the underside coloration has been emphasised. With one or two exceptions, in a very long series, the ground-colour in *suk* is a cold stone-grey.

Another important point is the food preference or even limitation ; for one cannot transfer larvae from *Acacia* to *Albizzia* or *vice versa.* The selective agent is the female parent.

Material Examined.

Beside the type material deposited in the British Museum we have critically examined a very long series of males and females in our collections, all from Karamoja and Suk. We tentatively place as *Ch. viola suk* the transitional specimens from Ukambani and Masai, all bred on *Acacia mellifera*, but they are not identical, having a browner ground-colour to the underside ; they represent a bio-ecological strain.

(vi) *Charaxes viola chanleri* Holland, 1895.

Charaxes viola chanleri Holland, 1895, type loc. Jombeni, N.E. Mt. Kenya.

Founded on a male ; female described by Holland, 1896, type loc. Jombeni, N.E. Mt. Kenya.

Description and Taxonomy.

Male : Nearest to *Ch. viola picta* both above and below. Two to three subapical white spots and a large blue spot in the cell towards apex, and between these two white spots a large subcostal and a small one below. *F.w.* lunules large and conspicuous, glaucous grey-green. *H.w.* marginal lunules above upper tail with just a slight red tinge in centres, and greenish to anal angle. Submarginal lunulate marks bluish-white, and internal to these a wavy green line from anal angle to 4–5. Tails short. *Uns.:* Ground-colour clayish-brown with dark markings very fine. Ground-colour quite different from *viola kirki* or *viola suk* but nearer to *viola picta.*

The female and two others associated by Holland with the male *chanleri* came from Jombeni area (not Kikuyu as suggested by Rothschild (*op. cit.*)). Dr. Holland says, " as to the exact localities from which the specimens (six males and three females) came I have no certain knowledge. Mr. Linnell writes that he was informed by Mr. Chanler that the greater number of the specimens were taken upon the Jombeni Range, N.E. Mt. Kenya." The female is described by Holland as follows :

" The upperside of the palpi is black, the upperside of the thorax and abdomen is dark fuscous. The lower side of the palpi and pectus white. The lower side of the thorax and abdomen brownish-grey. Legs unicolorous. The primaries are fuscous at the base and on the outer margin, the fuscous shade deepening into black toward the centre of the wing and the outer angle. The wing is traversed from the costa before the apex by a band of discal spots, gradually increasing in size from the costa to inner margin. The four uppermost spots are curved outwardly in a bent series ; the four lower spots are oblong quadrate. All are ochre-yellow except the two nearest the inner margin which are washed with white. In addition to this series of spots there are two yellowish spots beyond the cell and a small yellow spot at the lower outer angle of the cell. The secondaries are coloured at the base as the primaries with the inner margin dark fawn coloured. The macular band of the primaries is continued across the secondaries as a white band gradually diminishing in width toward the inner margin, and laved with blue on either side toward the extremity. The outer margin is broadly black beyond the discal band. The wing is bordered from vein 4 upwardly by light brown and inferiorly toward the anal angle by glaucous green, produced upon the two tails projecting from veins 2 and 4. These tails as well as the whole outer margin are edged by a very fine black line. Just within the light brown and greenish marginal border is a submarginal series of bluish-white linear spots on the interspaces, bordered externally by black from vein 4 to the anal angle.

" Upon the underside the wings are marked as in the male save that the broad macular discal band of the primaries and secondaries is reflected from the upperside, and owing to the greater size of the wings in the female the spots and markings are more widely separated. Expanse 65–70 mm. Type No. 56, U.S.N.M."

Breeding.

There is no record of this subspecies having been bred.

Habitat and Distribution.

This subspecies is found in the savannah woodland and near forest edges in the lower Meru area and the Jombeni Range to the Upper Tana River. Its known distribution is thus rather restricted. Records of *chanleri* from Nairobi and Kikuyu and Kibwezi are referable to *viola kirki*. From photographs of the type female received recently from the United States National Museum this subspecies appears to be identical with *Ch. viola picta*. The distribution would, however, be peculiar, and for this reason we prefer to retain it for the time being.

Material Examined.

Material examined includes eight topotypical males, including a paratype from the original Chanler series from Jombeni, in Coll. van Someren. It is also represented in Coll. Barton Eckett, Nairobi, from Lower Meru.

(vii) *Charaxes viola phaeus* Hewitson, 1891.

The following forms are discussed below :

♀ f. *phaeus* Hewitson, 1891, type loc. Delagoa Bay.
♀ f. *manica* Trimen, 1894, type loc. Manicaland.
♀ f. *coryndoni* Rothschild, 1900, type loc. Ganzangula, Upper Zambesi.
♀ f. **chintechi** f.n., type loc. Chintechi, Nyasaland.
♂. Described by Rothschild, 1900 (as *Ch. cytila*), type loc. Bandawe, Nyasaland.

Description and Taxonomy.

It may seem, at first sight, unwise to link *phaeus* and *manica* with the species *viola*, since the facies, at least in the females, is so very different. We are satisfied, however, that this is the correct interpretation. In the southern areas of its range *phaeus* entirely replaces *viola kirki* and *v. picta*. Moreover, in the extreme north of its range, i.e., Geita in N.W. Tanganyika and in the Suna area of S. Kavirondo, the males tend to be transitional between *picta* and *phaeus* in that they are more heavily spotted and less red below than typical *phaeus* of Nyasaland. In the South Kavirondo area there is contact with *picta*.

It inhabits the same type of country as *viola*, i.e., open semi-dry savannah, and it is significant that throughout its range the facies of the female forms have been modified to resemble the dominant and powerful *Charaxes bohemanni* Felder. The larval food-plants are species of *Entada*, as with *picta* and *kirki*.

Male (= *cytila* Rothschild) : Normally less heavily spotted above than in other subspecies ; a strong greenish sheen and greyish margins to *f.w.* ; always dark reddish below. Size usually smaller. Very similar to *Ch. fulgurata* Aurivillius, but in this species the submarginal spots of *f.w.* are joined to form a more or less strongly lunulate line and underside is light clay-coloured.

Two specimens from Vumba Mts. (*B. D. Barnes*) and one from Turiani (central Tanganyika Territory) (*T. H. E. Jackson*) differ from typical *phaeus* as follows :

Ups.: Blacker ; lacks entirely the grey-green apical marks and marginal lunules less distinct. Blue spots in *f.w.* normal. *Uns. :* considerably darker, a deep purply chocolate-brown as against a chocolate-brown with a slight purply flush ; submarginal series of contiguous red and green lunules show up more distinctly against the darker ground.

The female forms *manica* Trimen and *phaeus* Hewitson need no re-description here, but we draw attention to a form in the British Museum (Natural

History) from Chintechi and Mt. Mlanje areas of Nyasaland, which will require to be bred before it can be placed with certainty. Several of these females of the form *manica* have yellow subapical spots and two yellow discal spots beyond the end of the cell. In others, the double row of light spots in the fore wing are yellow and joined across to form yellow rays. Finally there are four specimens of a very distinct form described below :

♀ f. **chintechi** f.n.

Up.: F.w. basal area blue as in other forms, thereafter a short yellowish-white discal band 12 mm. wide at hind margin, then tapering across 1b and ending in a single quadrate spot in 2–3. Two small yellowish streaks in 7 and 8 beyond the cell and a small yellowish disco-cellular fleck ; a row of small yellowish submarginal and subapical spots as in other forms. Discal band distally edged with blue. *H.w.* as in female *phaeus*, but with traces of a whitish discal band across centre of wing. *Uns.:* Ground-colour dark reddish as in *phaeus*. *F.w.* discal white band is prominent in type specimen and there is also a trace of a narrow white band in *h.w.* Other two specimens entirely dark reddish-brown. This is a normal variation in the *ethalion-etheocles-viola* group. Expanse 65–70 mm.

Holotype ♀, Nyasaland : Chintechi (*Lloyd* leg.) (Joicey Bequest). Two paratypes also from Chintechi and one from Limbe, Nyasaland (Rothschild and Levick Bequests). All in British Museum (Natural History).

Breeding.

A female *phaeus* was observed laying on *Entada* sp. in the Suna, Kisii district, of West Kenya. The eggs were collected and the larvae duly emerged, but they refused to feed on the local *Entada abyssinica* of the Elgon area, and all died. This subspecies was bred by Dollman in N. Rhodesia on Musasi, Musubo and Kafundula (Leguminosae). (Attempts to find the scientific names of these plants from their native names have failed.)

Habitat and Distribution.

This species frequents the open savannah and orchard country. It occurs in the Suna and Chepalungu areas of west Kenya and in Geita, N.W. Tanganyika Territory ; in Nyasaland, P.E. Africa, North and South Rhodesia, Katanga, and Angola.

Material Examined.

The female forms occurring in various areas as represented in the British Museum and the authors' collections are as follows :

West Kenya, Suna area . .	f. *phaeus*.
Tanganyika Territory (Geita) .	f. *phaeus*, *manica*, *coryndoni*.
Nyasaland	f. *phaeus*, *coryndoni*, *chintechi* and *manica*.
Katanga and Angola . . .	f. *manica*, *coryndoni*.
P.E. Africa	f. *manica*, *phaeus*.
Rhodesias	f. *manica*, *phaeus*, *coryndoni*.
Transvaal	f. *coryndoni* (one in British Museum (Natural History).

We have also seen one male from Umtali, S. Rhodesia (*B. D. Barnes*) which appears to be typical *phaeus* Hewitson (=*cytila* Rothschild). A second specimen from the Vumba Mts. (*B. D. Barnes*) agrees with specimens from the same locality in the author's collections. One specimen from Turiani in the Uluguru Mts., Tanganyika Territory (*T. H. E. Jackson*), is temporarily placed here.

Mimetic Associations (Charaxes viola *and subspecies*).

The extent to which mimetic patterns and coloration have evolved in females of this species presents some curious anomalies. The *viola* pattern and coloration, so strongly developed in *viola viola*, *viola picta*, *viola suk* and *viola kirki*, do not appear to be influenced to any marked degree by the presence of more robust *Charaxes* species within their range and distribution, although it has been suggested that *C. epijasius* Reiche is the model in the West and east to Uganda. Nevertheless, there is a marked similarity between the form *daria* and the larger species which fly with it, viz., *Ch. achemenes monticola* Joicey and Talbot and *Ch. hansali baringana* Rothschild. There is also a marked similarity between the form *rogersi* and the larger species *Ch. pelias saturnus* Butler and the smaller *Ch. achaemenes achaemenes* Felder and *Ch. guderiana* Dewitz. There appears to be no direct model, however, for the *kirki* and *albifascia* forms within their range. It is remarkable therefore to note the very marked similarity between the various female forms of *viola phaeus* and the dominant powerful *Ch. bohemanni* Felder throughout the range of the two species.

It should be noted, however, that *Ch. bohemanni*, which is a rare species along the Kenya Coast, has not influenced the females of *Ch. viola kirki* in that area.

Before leaving *Ch. viola* and its subspecies, mention must be made of the following specimens in the British Museum which obviously belong to this species, but as yet cannot be placed with certainty :

(*a*) A single very small male from S.W. Africa with blue subapical and cell spots and a very pale underside.

(*b*) A series of six males from the upper Zambesi (no females). They are small, with bluish spots above, and with a silvery underside traversed by red and green post-discal lines ; a very silvery discal line and a white submarginal line.

Through the kindness of the Director, I was able to examine a long series from Katanga of *etheocles* (sens. lat.) in the Musée du Congo Belge at Tervuren. Most of the species mentioned in this paper were represented and in addition there is an interesting race of *viola*, similar to *picta*, but in which the *f.w.* band is purplish-brown and the *h.w.* band is mauve. (Jackson.)

Charaxes fulgurata Aurivillius, 1899.

The following forms have been described :

♂ f. *fulgurata* Aurivillius, 1899, type loc. Angola.
♀ f. *lunigera* Rothschild, 1900, type loc. Angola.
♀ f. *mima* Riley, 1921, type loc. N. Rhodesia.

Description and Taxonomy.

This species was considered to belong to *Ch. viola phaeus* until both were bred by Dollman in N. Rhodesia in 1917 and shown to be distinct.

Ch. fulgurata can be distinguished from *viola phaeus* by the row of submarginal lunules in *f.w.* in both sexes in place of the discrete spots of *phaeus*. *Uns.:* Light clay-coloured whereas in *phaeus* it is always reddish.

Breeding.

Dollman found that this species invariably laid on a species of *Acacia* called Kabulwebulwe (native name).

Mimetic Associations.

This species flies with *Ch. viola phaeus*, which it closely resembles in both sexes. Female form *lunigera* is very similar to *manica*, and female form *mima* to female forms *coryndoni* and *phaeus*. The primary model is *Ch. bohemanni*.

Habitat and Distribution.

This species inhabits the open savannah country where it flies with its model.

Material Examined.

There are examples in the British Museum from N. Rhodesia, Katanga, and Angola. A series of males from the Vumba Mts., S. Rhodesia (Coll. Jackson), seem to belong to this species. We have also examined a male from Vumba Mts., kindly lent to us by B. D. Barnes.

Charaxes aubyni Poulton, 1925.

♀ f. *aubyni* Poulton, 1925, type loc. Dabida, Teita Hills, Kenya.

Description and Taxonomy.

This very distinct species was originally taken by the late Canon St.Aubyn Rogers on the Teita Hills, and the female was described by Prof. Sir Edward Poulton as a form of *Ch. etheocles* Cramer. The male was referred to as like *chanleri*. A description of the associated male was given by van Someren and Rogers (*op. cit.* : 266, fig. pl. CXL), but no type was cited.

Male : General colour deep black with a greenish sheen ; costa broadly green at base. *F.w.* spotting as in *Ch. viola kirki*, two yellowish subapical spots, a yellow postdiscal spot with a dot below it, a blue spot toward apex of cell. Marginal lunules broad and greyish ; traces of a row of greenish submarginal spots. *H.w.* marginal lunules very broad and distinct yellowish-green from anal angle to vein 2, thereafter strongly red. A row of yellowish-green submarginal spots, those of 1b, 1c being strongly blue ; and internal to this a wavy greenish line. Tails yellowish-green edged with black and black tipped, and very long ; that on vein 4 is 7 mm. and at vein 2, 5 mm. *Uns.:* very similar to *viola kirki* but ground-colour darker brownish grey ; the black submarginal spots in 1b and 2 very large and prominent and the green submarginal line on *h.w.* broadly edged with dark brown distally. Expanse, average 60 mm.

Neallotype, ♂, Kenya : Wusi, Teita Hill, i.1947 (*J. G. Williams* leg.). In the British Museum (Natural History).

Female : Redescription not required, but it should be mentioned that pattern is very similar to that of females of *Ch. ethalion*, *viola kirki*, or *etheocles*, but light areas creamy-yellow when fresh. The series of postdiscal spots in *f.w.* above remain discrete from costa to 2 ; discal series very broad in 1a, 1b, then tapers rapidly to 3. An unusual variant has the two series of spots joined in the form of rays right up to area 6. Basal portions of *f.w.* and *h.w.* with a strong green sheen. Marginal lunules above upper tail strongly red ; tails very long. *H.w.* band strongly suffused with greenish on either side.

Breeding.

The species was first bred by Rogers, the offspring being two *aubyni* females and one male. The food-plant was stated to be *Albizzia* sp. It was subsequently bred by van Someren on *Albizzia sassa,* and some larvae, on transfer to Nairobi, were raised on *Albizzia gummifera.*

The larvae are generally similar to those of *Ch. viola kirki,* but larger ; the horns on the head shield are long and slender and slightly incurved at the top. A larva ready to pupate was taken on *Albizzia sassa* by R. E. V. Saunders, Ngong Rd. ; a female *aubyni* duly emerged. This was the first *aubyni* female to be obtained outside the Teita Hills area. Two more females were subsequently taken while laying on *Albizzia sassa* by B. Barton Eckett, Ngong, Nairobi.

Mimetic Associations.

This species meets *Ch. viola kirki* and *Ch. etesipe tavetensis* on the edges of the forests on the Teita Hills and adjacent ranges ; it flies with *Ch. ethalion, Ch. catachrous contrarius* and *Ch. pembanus usambarae* subsp. n. on the Usambara and Unguru Mts.

It also flies with *Ch. ethalion* and *Ch. viola chanleri* along the forest margins at Meru, Mt. Kenya ; here it also meets with *Ch. etesipe gordani* van Someren. A distinct race of *aubyni* occurs on Mt. Mlanje, Nyasaland, where it flies with *Ch. ethalion* and *Ch. viola phaeus.* The female resembles, somewhat, female form *ethalion*, but it bears a closer likeness to *Ch. brutus natalensis* Staudinger, and more so to the females of *Ch. etesipe tavetensis* and *Ch. etesipe gordani* in their respective ranges.

Habitat and Distribution.

This species occurs in forests on high ground where its food-plant, *Albizzia,* is plentiful, but since this tree is more often associated with damp places at forest edges and glades, the butterfly is often noted outside forest and is frequently taken at fermenting sap of trees well away from forest.

For a long time it was known only from the Teita Hills, but recent collecting has shown that it occurs on the adjacent ranges of Mbololo and Sagala and also on Kilimanjaro and in the Usambara and Unguru Mts. of Tanganyika Territory. It occurs in a slightly different form in the Nairobi area and at Meru, Mt. Kenya. A distinct race is found on Mt. Mlanje, Nyasaland, but so far only males have been taken. A female, sent to us for examination by Mr. B. D. Barnes, taken on the Vumba Mts., S. Rhodesia, appears to belong to this species. It differs from the typical female *aubyni* as follows :

Light areas creamy-white instead of creamy to yellowish ; below, ground-colour paler, more whitish and less tinged with brown. Agrees in size and shape with *aubyni.*

No racial forms of *Ch. aubyni* have been described, but from the evidence of material examined it would appear that the more southern representatives from Mt. Mlanje, Nyasaland, and from the Vumba Mts., S. Rhodesia, constitute a distinct race. We are, however, handicapped by lack of female material, especially that definitely associated with males by breeding.

We briefly mentioned that the specimens of *Ch. aubyni* from Nairobi area to Mt. Kenya differed from the nominotypical; the differences are as follows:

Ups.: F.w. spots smaller as a rule; marginal lunules above the upper tail not red but green, though there is a suggestion of red in one or two specimens. *Uns.:* Ground-colour slightly more brownish, the postdiscal series of greenish lunulate marks less wide and less prominent. These differences hold good in a series of 14 males and 3 females which, agreeing with nominotypical *aubyni* in general appearance, show the same differences found in the males.

A further series of males from Nyeri, Nairobi, Mau and Sotik (Kiptiget and Mwangoris) present interesting features. They agree with male *aubyni* in general size and shape and have equally long tails. They differ, however, as follows:

Ups.: Similar to males mentioned in the last paragraph above, but wavy greenish post-discal line in *h.w.* very strongly marked. *Uns.:* Main difference is in colour of underside, which is strongly suffused with reddish-brown.

With these males we associate a very distinctive female which has a similar reddish-brown underside, but the upperside pattern differs totally from that of *aubyni*, as follows:

Discal and post-discal series of spots in *f.w.* entirely free from costa to hind margin and relatively small; thus the band appears narrow; outer series ochreous to orange, inner series whitish with just a tinge of ochre distally. *H.w.* band very narrow, especially so in 5, and whitish with a very strong suffusion of blue in the disc. Basal halves of *f.w.* and *h.w.* strongly blue, not greenish.

There are two such females in our collections and six in the British Museum from Mt. Kenya and the Kikuyu Escarpment. We hesitate to designate this "species" by name since we have not bred male and female in one family.

We are indebted to Mr. K. M. Pennington of Natal for the loan of a very interesting female from the high veld, but unfortunately without an associated male. This belongs probably to the form or species mentioned above.

Material Examined.

Material examined in the British Museum comes from Kilimanjaro; Munisu, British East Africa (Delamere); from Lindi, Tanganyika Territory; Teita Hills (Dabida) and Taveta. There is a long series in the authors' collections from Teita Hills, Mbololo and Usambara Mts.; also from Nairobi, Meru, and Kiptiget, Sotik. Additional material from Nairobi and Meru has kindly been lent by Messrs. Barton Eckett and R. E. V. Saunders.

Charaxes pembanus Jordan, 1925.

This species occurs in two subspecies.

(i) *Charaxes pembanus pembanus* Jordan, 1925.

♂ *pembanus* Jordan, 1925, type loc. Pemba Island.

Represented by a single male in the British Museum (Rothschild Bequest) from Pemba Island. No female recorded.

Distinguished from *usambarae* subsp. n., described below, by underside which is red-brown with, on *h.w.*, a submarginal band of large red spots. *Ups.: F.w.* spots larger. Expanse as large as in *usambarae* and tails as long.

Female unknown, as is also the life-history. So far as is known, it is confined to the Island of Pemba.

(ii) *Charaxes pembanus* **usambarae**, subsp. n.

Male : Ups. : F.w. blue spots smaller than in nominotypical subspecies in most specimens, but an extra small blue spot at the end of the cell. *H.w. :* Small blue submarginal spots larger and become streaks toward anal angle ; anterior dull red portion of marginal band broadly edged with greenish blue. Tails very long, as in the typical *pembanus*, 9 mm. on vein 4 and 10 mm. on vein 2 (the latter missing in the type of *pembanus*).

Uns.: Very dark mahogany ; *f.w.* much as in typical race, but in *h.w.* the broad square submarginal red spots replaced by small red-brown lunules and altogether missing in 6–7. The green lunulate line proximal to this is much broader and the most pronounced feature in the wing. The row of bright blue submarginal spots, edged proximally with white, larger. Anterior half of the margin, which in *pembanus pembanus* is plain dark red, is here edged on both sides with green. Margins of *f.w.* crenate and fringes white. Expanse 65 mm.

Female : Very similar to *Ch. ethalion* ♀ f. *rosae*, but distinguished by its larger size, strongly crenate margin to *f.w.* and longer tails. *Ups.: F.w.:* The white discal band narrower than in *rosae*, being 7 mm. broad at vein 2 as against an average of 9–10 mm. in *rosae*. Proximal edge of band rises vertically from inner margin to end of cell and then runs horizontally across it, thus forming two sides of a square. In *rosae* this edge is rounded. Distal edge of band rounded as in *rosae*, but narrower and irregular where it crosses the cell. An unusually interesting character is that the small black line in the base of cellule 4, common to all *Charaxes* of this group, but which is lost in *rosae*, is still present here and shows up prominently in *f.w.* band above. *Ups.: H.w.:* Discal band as in *rosae*, white with broad pale blue edges and of about the same width. *Uns.:* Ground-colour dark brown, much darker than in *rosae*. *F.w.* band as above, the black streak in cellule 4 being prominent. Black basal spot and streaks and black submarginal spots very sharply defined. On *h.w.* a narrow white discal band varying in width and intensity. Green submarginal band very marked just as in males. Tails very long, 12 mm. on vein 4 and 11 mm. on vein 2. Expanse 65–70 mm. (*rosae* from the same area about 47 mm.).

Holotype, ♂, Usambara, ex coll. Brabant. Joicey Bequest.

Allotype, ♀, same data.

Paratypes, 2 ♂, Usambara, Joicey Bequest, and Usambara ex coll. Grose Smith, 1910. 2 ♀ Usambara ex coll. Suffert, Joicey Bequest, and Bulwa, Usambara, also Joicey Bequest, all in British Museum.

This fine species cannot be mistaken ; its large size, strongly crenate margins to the fore wings, very long tails and very dark colouring above and below serve to distinguish it from all others.

Breeding.

Nothing is known of its food-plant or life history.

Mimetic Associations.

This species flies with *Ch. ethalion*, *Ch. catachrous contrarius* and *Ch. aubyni*, and also with *Ch. violetta* Smith and *Ch. cithaeron kennethi* Poulton. The female bears a strong resemblance to *Ch. ethalion* female form *rosae*, but the primary models are *Ch. violetta* and *Ch. cithaeron kennethi*.

Habitat and Distribution.

This a forest insect and is known only from the Usambara Range.

Material Examined.

A series of males from Amani, Usambara, in the authors' collections.

Charaxes cedreatis Hewitson, 1876.

Two subspecies are known :

(i) *Charaxes cedreatis cedreatis* Hewitson.

♀ f. *cedreatis* Hewitson, 1876, type loc. Fernando Po.
♀ f. *protocedreatis* Poulton, 1925, type loc. Uganda.

The type is a female ; the male was described by Rothschild, 1900 (as *Ch. lutacea*), type loc. Fort Beni, Congo Belge.

Description and Taxonomy.

This species is very distinct and is remarkably constant throughout its range. The chief characters distinguishing the male from others of the group are as follows :

Male : F.w. more elongate, longer in respect to the breadth than in all other species except *Ch. virilis* Rothschild. A strong bluish-green basal sheen. Spots usually limited to one subapical, one post-discal, and one at end of the cell ; a few examples have an extra subapical spot. Marginal greyish lunules well separated by dark veins. On *h.w.* always a prominent row of elongate white submarginal spots ; marginal lunules above upper tail almost invariably broadly red-brown. *Uns.:* Dark brown and strongly variegated, more so than in well-marked examples of *Ch. etheocles* ♂ f. *ephyra* Godart (*hollandi* Butler).

Female : Differs from all others of the group. *Ups.: F.w.* basal half tawny olive, distal half black, separated by a curved row of large white linear spots from cell to hind angle ; *h.w.* tawny-olive with a broad black border carrying a complete row of white crescentic spots ; marginal border strongly reddish above upper tail.

The form *protocedreatis* Poulton differs from typical *cedreatis* in being a darker olive above but with a light yellowish post-discal zone internal to the black border.

Breeding.

Numerous families have been bred from known female parents and the resultant offspring have been true to type, viz., female *cedreatis* and male *lutacea*. The form *protocedreatis* occurs as an occasional variant.

The food-plant of the larva and the only tree on which the females have been seen laying is *Albizzia grandibracteata* (Luganda, Nongo). The Baganda distinguish two types of this tree, " male and female," one with hard, the other soft wood. Most of the families were bred in the east Uganda area of Jinja and east Elgon. The horns of the headshield of the larvae are short, slightly incurved and dark brown ; the head-shield is quadrate.

Habitat and Distribution.

Ch. cedreatis is associated with forest, but since its food-plant, *Albizzia grandibracteata*, is found mainly along the margins of forest and in patches of more open type, females are more often noted outside heavy forest; moreover, where forest has been cleared for cultivation, the *Albizzia* stumps are often left and suckers grow from nearly every root left in the ground. *Ch. cedreatis* is thus often seen laying on *Albizzia* saplings in clearings and native "shambas".

Material Examined.

The species has a wide distribution and specimens examined include the following:

British Museum: Nigeria, Gaboon, Gold Coast, Ivory Coast, French Guinea, Fernando Po, Cameroons, North Angola, Congo, Uganda, Kenya west of the Rift.

Authors' collections: East Congo Belge, Ituri, Uganda, West Elgon; Kenya: East Elgon, Nandi, Kakamega, Lumbwa, Ravine, Mau, Cherangani.

(ii) *Charaxes cedreatis vetula* Rothschild.

The type is a female, type loc. Ogowe River, West Angola. Male described below.

Male: Ups.: Very like the nominotypical subspecies, but slightly smaller; spots on *f.w.* tend to be larger. In S. Angola males are smaller and darker. *Uns.:* Usually less strongly variegated and thus more like *Ch. etheocles* ♂ f. *carteri* Butler.

Female: This sex is rare in collections. *Ups.:* Tawny-olive area of typical *cedreatis* replaced by blue, except in basal area of both wings, which are broadly black. *F.w.* post-discal band white, and varies in width from 2·5 mm. to nearly 5 mm. in areas 4–5.

Neallotype, ♂, TANGANYIKA TERRITORY: Geita, viii.1937 (*T. H. E. Jackson*). In British Museum (Natural History).

Breeding.

There are no records.

Habitat and Distribution.

This subspecies is found in and around forest margins and often in savannah or orchard country.

Mimetic Associations.

Ch. cedreatis cedreatis flies with *Ch. etheocles* Cramer, *Ch. catachrous* Staudinger and the large species *Ch. tiridates* Cramer, *numenes* Hewitson, and *bipunctatus* Rothschild. The female is a remarkable mimic of the females of these three powerful species.

Since the range of *Ch. cedreatis vetula* is to the south of *cedreatis cedreatis* it comes under the influence of *Ch. bohemanni.* This is particularly the case in the Geita area of Tanganyika Territory. It should be noted, however, that to the east, in the Chepalungu-Sotik area, *bohemanni* is not plentiful, but *vetula* occurs. Moreover, both *Ch. tiridates* and *numenes* are present in some numbers.

Material Examined.

In the British Museum: Six males from Quirimbo, S. Angola; seven males from Mpala, Tanganyika Territory; the type female from Ogowe River, W. Angola.

In Coll. Jackson: Four males and one female from Geita, Tanganyika Territory.

In Coll. van Someren: Two females and one male from Chepalungu Forest, West Kenya.

In addition, two males from Mwanza in the British Museum and six males in Coll. van Someren from S. Kavirondo are doubtfully placed here. They differ from typical males in being less spotted on the fore wing above, and in almost lacking any trace of marginal red above the upper tail. The underside is more uniformly brownish, but with a strong well-marked yellowish-green and dull red wavy line from anal angle to costa.

A long series of males (no females have been taken) from the high Kigezi country of Western Uganda appear to belong to this species. They are characterised by the strong development of the blue submarginal spots of the fore wing and the greenish-blue submarginal band on the hind wing, and thus closely resemble Staudinger's figure of *Ch. kheili* (1896, *Iris*, **9**: 216). Unfortunately there are no specimens of the latter either in the British Museum (Natural History) or at Tring, but, through the kindness of Prof. Herring, who forwarded the type from Berlin, the genitalia were compared with those of the Kigezi males and with *cedreatis cedreatis* and *cedreatis vetula.* No significant differences were found between any of these. There are four further examples of *Charaxes kheili* in the Musée du Congo Belge, Tervuren. A single damaged female of the Kigezi race in coll. van Someren, is of the *vetula* type, but more examples are required before this subspecies can be described.

Charaxes catachrous Staudinger, 1896.

The type is a male, type loc. Cameroons. Female described below.

Description and Taxonomy.

The males of this species present certain characters which are constant throughout its range, viz., the colour of the underside, which is silvery in the basal two-thirds, flanked by brownish distad in the fore wing. The hind wing is silvery in the basal half and brownish in the outer portion and this is traversed by a continuous row of red and green lunules which form a prominent feature. Two subspecies are known, an eastern and a western.

(i) *Charaxes catachrous catachrous* Staudinger.

Male: Ups.: Very similar to male forms *ephyra* and *carteri* of *Ch. etheocles,* but more intensely black above. *Uns.:* Silvery-white basally, with a silvery discal band on both wings.

Since the female has hitherto been confused with female *etheocles* and not specifically associated with male *catachrous* Staudinger, in any description, we give the following:

Female: Pattern above generally similar to that of *Ch. etheocles* ♀ f. *etheocles,* but differs in that the discal and post-discal series of spots in *f.w.* are creamy to ochre yellow; in typical female *etheocles* they are ochre to orange (white or bluish-white in eastern Uganda). In *h.w.* the median band narrower, as a rule, and shaded with a deeper blue; submarginal series of white spots very prominent. *Uns.:* Ground-colour silvery-white as in male; white median band broader than in *etheocles* and does not taper off so rapidly toward the hind angle. These differential characters remain constant over a wide range.

Neallotype, ♀, UGANDA: Bwamba, vi.1942 (*T. H. E. Jackson*). In British Museum (Natural History).

Breeding.

No families have been bred. Odd pupae were taken in the Bwamba Valley in 1946, but since a larva ready to pupate wanders for some distance before selecting a suitable pupating site, one cannot with certainty regard the plant on which it pupates as its food-plant.

Mimetic Associations.

This species flies with *Ch. etheocles*. The female is a mimic of female *Ch. ameliae* Doumet.

Habitat and Distribution.

This species is associated with forest and is most plentiful in the western portions of its range, especially the eastern Congo and Western Uganda. It becomes scarce in its eastern limits.

Material Examined.

Material examined in the British Museum comes from Nigeria (one male); Old Calabar (one female); Cameroons (a series of both sexes); Congo and Uganda. There is a long series of both sexes in the authors' collections from Bwamba and Budongo in Western Uganda; also from east Congo; and a few males from eastern Uganda to Kakamega.

(ii) *Charaxes catachrous contrarius* Weymer, 1907.

♂ *contrarius* Weymer, 1907, type loc. German East Africa.
  syn. *subargentea* van Someren, 1932, type loc. Rabai.
♀ f. *contrarius* (described below).
♀ f. **pseudorosae** f.n.

Description and Taxonomy.

An excellent figure of the male is given by Weymer in *Iris*, **20** : 44. This depicts the silvery underside and establishes its identity with *subargentea* van Someren, 1932, beyond any doubt.

The differences between male *catachrous catachrous* and *catachrous contrarius* are as follows:

Ch. catachrous catachrous.	*Ch. catachrous contrarius.*
Size larger, *ca.* 57 mm.	Size smaller, *ca.* 53 mm.
Ups. marginal grey lunules rarely present, small.	Marginal lunules larger and always present.
Spots on *f.w.* small, subapical, vestigial or absent; blue or greenish-blue.	Spots larger, pale blue, or whitish.
Little sheen to general surface, base *f.w.* costa greenish.	Strong sheen, bluish; base *f.w.* costa strongly blue.
Submarginal greenish line *h.w.* absent.	Submarginal greenish undulate line almost always present.
H.w. marginal red and green border vestigial, usually absent.	*H.w.* marginal red and green border always present, strong.
Tails shorter.	Tails longer.

♀ f. *contrarius* Weymer: Very similar to yellow-marked female *ethalion* Boisduval. A few may be white marked. Readily distinguished from female *ethalion* by its larger size, more falcate and crenulate fore wings; the outer margin in *ethalion* is almost straight. General pattern and placing of spots very similar above, but silvery-white underside of *contrarius* quite different from brownish basal areas in *ethalion*.

Neallotype, ♀, TANGANYIKA TERRITORY: Amani, Usambara Mts., iv.1950 (*T. H. E. Jackson*). In British Museum (Natural History).

♀ f. **pseudorosae** f.n.—Pattern as in ♀ f. *rosae* of *ethalion*, but differing slightly in that distal edge of fore wing bar is not so rounded, but is cut off and shortened in area 3–4. Margin to fore wing more falcate. Larger as a rule, and with a silvery underside as in the male, not brownish as in *rosae* of *ethalion*.

Holotype ♀, TANGANYIKA TERRITORY: Amani, Usambara Mts. (*T. H. E. Jackson*). In British Museum (Natural History).

Breeding.

This subspecies has not been bred.

Mimetic Associations.

This species flies with *Ch. ethalion*, *Ch. aubyni* and *Ch. pembanus usambarae*. The two female forms are very like female forms *ethalion* and *rosae* of *ethalion*, but the primary models are *Ch. cithaeron* and *Ch. violetta*.

Habitat and Distribution.

This insect is confined to the forest area of the Kenya and Tanganyika coast and the Usambara Mts.

Material Examined.

Material examined in the British Museum comes from Ndzovuni (1 specimen, *Rogers*); Mombasa (one specimen ex Coll. Grose Smith (Joicey Bequest)); a series of both sexes from Usambara. In the authors' collections there are a female *pseudorosae* and one *contrarius* from Kilifi, males from Shimba Hills, Rabai and Sekoke Forest and a series of both sexes from Usambara Mts.

Charaxes etheocles Cramer, 1777.

The following forms need discussion:

♂ f. *ephyra* Godart, 1823, type loc. "West Africa."
  syn. ♂ f. *hollandi* Butler, 1893, type loc. Sierra Leone **syn. n.**
♂ f. *carteri* Butler, 1881, type loc. Accra, Gold Coast.
♀ f. *violacea* Rothschild, 1900, type loc. Ogowe River, West Angola.
♀ f. *etheocles* Cramer, 1777, type loc. Sierra Leone.
♀ f. *alladinis* Butler, 1869, type loc. ? (None given.)
♀ f. *regalis* Rothschild, 1900, type loc. Sierra Leone.
♀ f. *ochracea* Rothschild, 1900, type loc. (probably French Congo).
♀ f. *fulgens* Rothschild, 1900, type loc. Sierra Leone.
♀ f. *seriata* Rothschild, 1900, type loc. Cameroons.
♀ f. *carpenteri* Poulton, 1918, type loc. Kakindu, W. Uganda.
♀ f. *evansi* van Someren and Rogers, 1932, type loc. East Elgon.

Description and Taxonomy.

The type of this species, ♀ f. *etheocles* Cramer, came from Sierra Leone. An examination of the coloured drawing in *Papillons Exotiques* **2**, Plate 119, shows that it does not exactly agree with any known form, and the type has long since been lost. The figures given by later writers, Herbst (1790, *Naturg. Schmett.* **4** : 65) and Thon (1837, *Naturg.* **1** : 37), are copies of the original figure.

The original drawing seems to agree best with the upperside of female *Ch. catachrous catachrous*, but there are no examples of this species from Sierra Leone. The underside agrees much better with the form found in Sierra Leone, of which there is a long series in the British Museum. We are forced to the conclusion, therefore, that Cramer's figure is inaccurate and that the name *etheocles* Cramer must be applied to those females which agree closest to his figure and come from his type locality, viz., Sierra Leone.

Similarly, there is some confusion as to the identity of the male form *ephyra* Godart, which has priority over all others. In the description the author states that it differs from " *etheocles* " in being smaller and " sans bande blanche de part et d'autre." Godart was therefore comparing it with the female type from Sierra Leone. The locality given is merely the West Coast of Africa.

An examination of the material in the British Museum shows that, apart from male form *violacea* Rothschild, which has a strong violet sheen, and is of uncertain affinities, only two forms can be distinguished amongst the males ; these are *hollandi* Butler and *carteri* Butler, the former with underside variegated, and the latter plain. The uppersides are variable throughout and not diagnostic. It follows therefore that one or other of the above must sink to *ephyra* Godart. We have consulted the authorities of the British Museum on the subject and they are of the opinion that this must be *hollandi* Butler, and there is some evidence in support of this view. The majority of the males from the West Coast are *hollandi* ; the whole series from Sierra Leone (type locality of *etheocles* Cramer) belong to this form, whilst *carteri* is rare, becoming commoner toward the east, until in western Kenya it almost predominates. It seems, therefore, fairly certain that Godart's *ephyra* belonged to the *hollandi* form.

♂ f. *ephyra* Godart (*hollandi* Butler).

♂ f. *carteri* Butler.

Ups.: Black with little or no sheen. *F.w.* spots usually confined to one subapical, one post-discal and one at the end of the cell, but a second subapical may be present. Grey marginal lunules small or absent. A row of small submarginal spots on *h.w.* with, occasionally, a wavy green line proximad. *Uns.: ephyra* variegated, *carteri* plain ; intermediates occur.

♂ f. *violacea* Rothschild : Exactly similar to above, but with a strong violet sheen.

♀ f. *etheocles* Cramer : *Ups.* : *F.w.* discal and post-discal series of spots yellow to ochreous ; upper series discrete or sometimes joined in the form of rays. *H.w.* band white with bluish edges. In the eastern areas of its distribution *etheocles* females tend to be paler spotted, the yellow is replaced by white or bluish-white. (Western Uganda to Busoga, and N.W. Kenya, S. Kavirondo.)

♀ f. *regalis*, Rothschild : *F.w.* discal and post-discal spots strongly ochreous, often fused to form rays.

♀ f. *ochracea* Rothschild : Whole of upper surface pattern suffused with orange, including *h.w.* band.

♀ f. *evansi* van Someren and Rogers : *F.w.* spots discrete in both series in a large number of examples, but may be conjoined up to 4–5. All spots strongly orange or orange tawny. *H.w.* discal band narrow and strongly bluish on both edges. Kenya, East Elgon to Mau.

♀ f. *alladinis* Butler : A large male-like form in which whole of upper side strongly purply-blue and pattern limited to a series of discal and post-discal blue spots in *f.w.* and a series of blue spots in *h.w.* The form *fulgens* Rothschild hardly merits a name : the type differs little from small examples of f. *alladinis*.

♀ f. *carpenteri* Poulton : Similar to *alladinis*, but usually smaller and bluer, and often with a blue discal band in *h.w.* An eastern representative of *alladinis* and rather unstable.

♀ f. *seriata* Rothschild : Very similar to *alladinis* in pattern, but is suffused with orange-brown, a feature common to female forms from French Congo and Cameroons.

Breeding.

Several families have been bred from known parents, i.e., f. *etheocles* and f. *carpenteri* in the Jinja area of Uganda. The offspring have either been *etheocles* or *carpenteri* or both forms in the one family : the males have been *carteri* Butler, or variegated below as in *ephyra* (= *hollandii*). The food-plants have always been *Scutia indica* and *Scutia commersoni*, but the head shield is slightly different. The horns are short, the centre ones strongly incurved and dark brown in colour. Several other families have been bred from female form *evansi*. The female offspring have always been form *evansi*, with no suggestion of transitional forms toward f. *etheocles*, in over a dozen large families. The males cannot be distinguished from *ephyra* and *carteri*, though predominantly the latter. The larvae are very similar to those of the Jinja area but the horns on the head shield are both dark brown. The food-plant is again *Scutia*.

Mimetic Associations.

This species flies with *Ch. virilis* Rothschild, *Ch. catachrous* and *Ch. cedreatis*. The models for the various forms are :

	Models.
♀ f. *alladinis* Butler	*Ch. tiridates* Cramer.
f. *fulgens* Rothschild.	*Ch. numenes* Hewitson.
f. *carpenteri* Poulton.	*Ch. bipunctatus* Rothschild.
f. *etheocles* Cramer	*Ch. ameliae* Doumet, ♀.
f. *regalis* Rothschild.	*Ch. imperialis* Butler, ♀.
f. *evansi* van Someren and Rogers.	*Ch. ansorgei* Rothschild, ♂ & ♀.

Poulton (1925, Mimicry in African Butterflies of Genus *Charaxes*. *Verh.* **3** *Int. Kongr. Ent.* suggests that *Ch. etesipe* Godart is the model for female f. *carpenteri* Poulton.

Insufficient is known of the French Congo, Gaboon and Cameroons orange-marked forms to be certain of the models, although Sir Edward Poulton (*op. cit.*) suggests female *Ch. cynthia* Butler as the model for f. *ochracea* Rothschild.

Habitat and Distribution.

Ch. etheocles is a forest insect, but since both its food-plants (in Uganda and Kenya at least) are associated with forest edges and clearings and secondary growth, females are frequently seen outside forest.

The species ranges from the West coast to western Kenya. The whole of this complex is treated, for the time being, as belonging to one polymorphic and highly mimetic species. There are indications, however, and some substantial evidence, that when more is known of the early stages (families bred from known parents), especially from West Africa, and of the distribution, it will divide up into well-defined geographical races, possibly, as follows:

(*a*) Ivory Coast, Old Calabar, Liberia, Fernando Po, Nigeria: females ***alladinis, etheocles, fulgens.***

(*b*) Sierra Leone: females *alladinis, etheocles, fulgens, regalis.*

(*c*) French Congo, Gaboon, and Cameroons: females *ochracea, seriata, etheocles* with orange suffusion.

(*d*) Congo, N. Angola, S. Sudan, Uganda, N.W. Kenya: females *etheocles* (pale form), *carpenteri.*

> *Note.*—The ♀ f. *etheocles* here mentioned differs from the western form and from ♀ *Ch. catachrous catachrous* by the fore wing spots being less tinged with yellowish, often bluish-white and by the hind wing band being shaded with greenish or greenish-blue.

(*e*) Kenya Highlands: High country west of the Rift, Mt. Elgon, Mau, Lumbwa, Ravine, Molo. The female is always f. *evansi.*

An interesting female in the British Museum from Eldoma Ravine (*H. R. Gallatly*, leg. 1912) has the fore wing as in *carpenteri*, but the hind wing has a conspicuous complete broad post-discal blue band. Another female from the same locality in Coll. van Someren is very similar but the hind wing band is slightly narrower and is shaded with orange distally.

Charaxes virilis Rothschild, 1900.

Charaxes virilis Rothschild, 1900, type loc. "West Africa."

The type is a female; male described by Jordan, 1920 (as *Ch. lenis*), type loc. Mulange, Mabira Forest, Uganda.

Description and Taxonomy.

The general shape of this species is reminiscent of *Ch. cedreatis* (= *lutacea* Rothschild), but it is smaller and both sexes can be distinguished by the brilliant blue sheen on the upper side of both wings; the under surface is almost uniform purplish-red-brown without variegation.

Male: Ups.: Apical spots usually absent, usually one large post-apical spot with a small dot below it; a conspicuous spot in the cell and all spots blue. Marginal lunules *f.w.* separated by dark veins, greyish-green. *H.w.* submarginal row of white spots very marked; marginal lunules above tail red, then greenish to anal angle. Some specimens with a greenish wavy line internal to submarginal spots. *Uns.:* Both wings purply-red-brown, post-discal line on *h.w.* prominent.

Female: This is male-like, but occasionally has a series of small post-discal blue spots in *f.w.*

Breeding.

There is a bred family in the Hope Dept., Oxford. Prof. Sir Edward Poulton wrote "that wild caught larvae were bred by Lamborn and Farquharson in Nigeria on *Adenanthera pavonina* (Leguminosae) producing only male-like females," and later states " these females are nearer to *virilis* than *alladinis*."

Mimetic Associations.

This species flies with *Ch. etheocles*, *Ch. cedreatis* and *Ch. catachrous*. The females mimic the males of *Ch. tiridates*, *numenes* and *bipunctatus*.

Habitat and Distribution.

This species is associated with forest and occurs from the West Coast to east Uganda. It is, however, comparatively rare.

Material Examined.

Material examined in the British Museum comes from Nigeria, the Congo and Uganda ; in the Hope Dept. from Nigeria and Uganda ; and in the authors' collections from East Congo, Uganda (mostly Mabira forest).

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MATSUCOCCUS PINI (GREEN, 1925) (HOMOPTERA, COCCOIDEA: MARGARODIDAE): BIONOMICS AND EXTERNAL ANATOMY WITH REFERENCE TO THE VARIABILITY OF SOME TAXONOMIC CHARACTERS.

By K. L. Boratynski, Ph.D., F.R.E.S.

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With 4 Plates and 7 Text-figures.

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INTRODUCTION.

Matsucoccus pini (Green) is at present the only indigenous scale insect found on pines in Great Britain, and the sole British representative of the interesting genus consisting of 17 known species (1 Japan, 1 China, 12 U.S.A., 1 Dominican

Republic, 1 France) all confined to pines (*Pinus* spp.).[1] Hitherto it has been known from a few adult females from Oxshott, Surrey, obtained by beating the branches of pine (*Pinus sylvestris*), and was originally described by E. E. Green (1925) under the name *Kuwania pini*, later (1926) recognised as congeneric with *Matsucoccus* Cockerell (1909). In 1928 H. Morrison expressed the opinion that *M. pini* is identical with the type species, *Matsucoccus matsumurae* (Kuwana, 1907). Since then, however, when some (six at present) American species had been recognised as serious pests of pines, more attention has been given to the genus. In 1939 H. Morrison published a preliminary description of ten new species, " . . . in order to make the names available to economic workers concerned with some of these species and in subsequent taxonomic and biological papers to make easier discussion of the various forms now recognised." In the same paper he observed that " the relationship of some of these species is so close that excellent insect material of all stages in quantity and much further study are needed for their proper characterisation, and especially for the establishment of a basis for the accurate differentiation of the species in any stage in which they may be encountered." Certain minute characters have been suggested and used (Morrison, 1928, 1939 ; McKenzie, 1941, 1943), and consequently the original description of *M. pini* became insufficient for its characterisation. The initial scope of the present study was therefore to amend and supplement the original description of the female with details now recognised as essential, and to describe the other stages hitherto not known.

Females of *M. pini* available to E. E. Green (1925) for study were collected in October (1923) and again in the following May and were considered as representing the same generation, the female hibernating in the adult stage. Preliminary observations on the biology of the insect in 1948 revealed that it has two generations a year, the spring generation hibernating in the larval stage. So far this is the first record of any species of the genus being bivoltine ; even *M. feytaudi* Ducasse from south-western France has only one generation in the year. This being so, the life-history and habits of all stages have been studied in detail.

Examination of a series of specimens revealed that the females of the two generations show quantitative differences in size and certain other characters. Some statistical analysis has been applied in order to determine the significance of these differences and the variability of the characters in the two generations. The results obtained provide some suggestions regarding the characters which could perhaps be used for defining the species within the genus.

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This work has been carried out in the Entomology Department, Imperial College of Science and Technology. The material has been collected and the field observations made at the College Field Station at Silwood Park, Sunninghill, Berks. It is my privilege to express my gratitude to the Director of the

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[1] Since this paper was written, Borkhsenius' book on the mealy bugs and scale insects of the U.S.S.R. (Borkhsenius, N.S., *Tcherveci i shchitovki S.S.S.R.*, Akademia Nauk S.S.S.R., Moskwa-Leningrad, 1950, 249 pp., 466 figs.), has become available, in which *M. pini* (Green) is recorded as occurring in the Leningrad area (U.S.S.R.). The characterisation of the adult female of the species given by Borkhsenius, obviously based on Russian specimens, shows that they represent a quite different species, probably a new one (Boratynski, K., 1952, *Ann. Mag. nat. Hist.* (12) **5** : 507–508).

Department and the Field Station, Professor J. W. Munro, for the opportunity to work there, and to him and Dr. O. W. Richards for their interest. I am also grateful to Dr. Richards and Mr. R. G. Davies for reading the manuscript and discussing some aspects of the work. My thanks are due to the Trustees of the British Museum (N.H.) and to Mr. N. D. Riley, Keeper of the Department of Entomology, for making available the specimens of *M. pini* in the Collection, and especially to Mr. F. Laing for his interest in my work, for valuable suggestions and for reading the manuscript. The identification by Dr. T. E. Hughes of the mites associated with *M. pini* is gratefully acknowledged.

II. MORPHOLOGY.

A. *Description of the Stages.*

Matsucoccus pini has two generations in the year and is parthenogenetic. Its developmental stages are as follows :

1. Egg.
2. 1st stage larva :
    - *a.* Crawler, motile immediately after hatching, and after settling changes considerably in size and shape without moulting to become—
    - *b.* Fully grown.
3. Intermediate (apodous) stage.
4. Adult female.

The eggs and the 1st stage larvae of the two generations cannot be distinguished. The individuals of the intermediate stage are also identical in the structural details of the spiracles, apparently the only obvious feature on which at this stage the separation of the more closely related species can be based. Assessment of the probable differences in size of fully grown individuals of this stage is impossible owing to considerable distortion of the insects under natural conditions. The adult females of the two generations differ in size and in the means and ranges of some measurable and numerical characters. The description of the female therefore shows wider ranges and greater variation of these characters than those exhibited by either of the two generations separately.

The description of each stage is based on 20 specimens, ten of each of the two generations, selected at random and treated together. As the essentials for the accurate differentiation of the species at various stages are not established, and in order to provide information which may in future be required, the descriptions here given record all the details observed. The drawings and figures have been made with camera lucida and accurately represent the specimens actually drawn. E. E. Green's original specimens of the adult female in the collection of the British Museum (N.H.) have been also examined. These include : (*a*) one Type slide containing two specimens collected in May, 1924 (spring generation), and (*b*) three slides containing several specimens collected in October, 1923 (summer generation). Among the latter there are only two specimens which are in a condition suitable for measurement. The characters of these four specimens fit well within the ranges of the two respective generations.

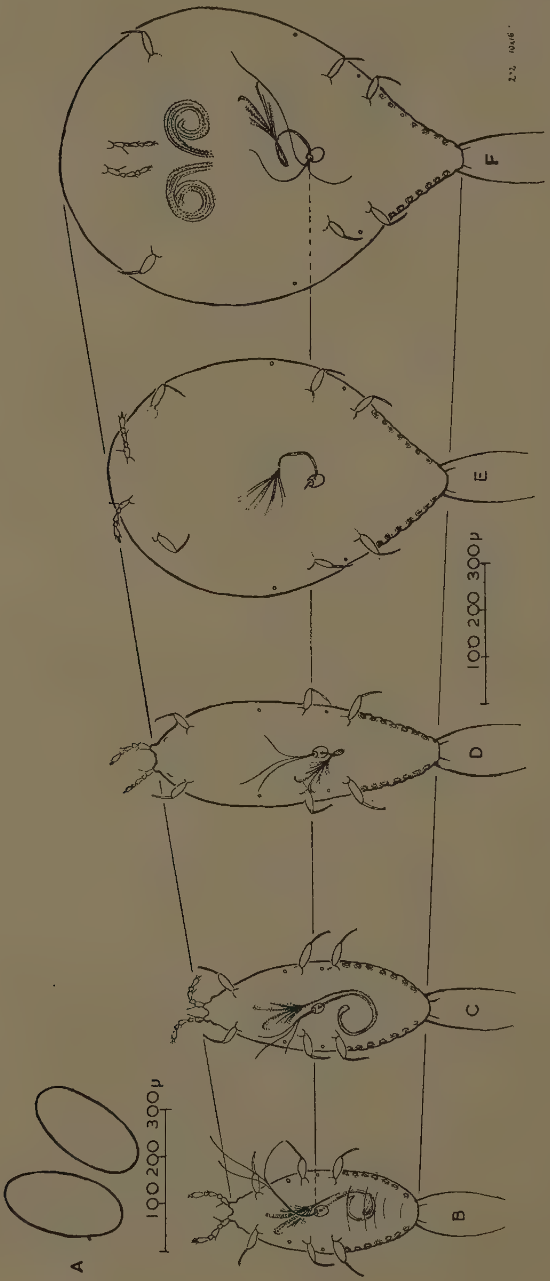
A
B
C
D
E
F
100 200 300μ
100 200 300μ

Fig. 1.—A, eggs; B–F, 1st stage larva, growth series.

1. The egg (fig. 1, a).

Elongate ovoid with both ends broadly rounded; length 260–280μ, average 275μ; width 100–120μ, average 112μ; colour amber-yellow, with smooth and shining surface. In the second half of the incubation period the red eye-spots of the developing embryo are visible through the egg-shell.

2. The 1st stage larva.

a. The Crawler Immediately after Hatching (Plate I, figs. A–K).

Body elongate, nearly parallel-sided, broadest across the metathorax and moderately flattened; anterior end tapering rather abruptly from the level of about half the distance between the anterior and middle coxae; posterior end narrowly rounded. Dimensions (mounted specimens): length 365–446μ, average 396μ; width 167–200μ, average 182μ. *Colour* of living specimens amber-yellow, turning brown after death. *Derm* membranous. *Antennae* (fig. B) six segmented, 105–122μ long, average 112μ, i.e., about two-sevenths length of body; situated at the slightly truncate anterior apex of body; bases proximate, the interval between about half width of 1st segment, which is about 25μ wide and 16μ long; 2nd segment oval, about 14μ wide and 20μ long; segments 3 to 6 slender (10–12μ wide), 3rd and 5th being short (about 6 and 10μ long respectively), the 4th longer (20μ) and the 6th longest (about 40μ), with distal one-third forming a constricted terminal prolongation. 1st segment bears one minute seta at base dorsally and one longer in middle of segment medially; 2nd with three setae in a circle across middle of segment and with one sensorium on distal end of segment dorsally; 4th with a single stout spine; 6th with two similar spines at base of constricted terminal part, four slender setae at tip of terminal prolongation, and with two distinct sclerotisations of the cuticle in form of slender pointed struts (*s*). No setae or spines on 3rd and 5th segments. *Eyes* distinct, on margins behind antennae; in living individuals of reddish-brown colour. *Legs* (figs. C–E) well developed, about the size of the antennae; anterior noticeably shorter and situated far in front of middle pair, distance between anterior and middle coxae being about twice that between middle and posterior pairs. Coxa normal, bulging from body; basal rim and points of articulation with trochanter sclerotised, elsewhere membranous. Trochanter incompletely separated from femur. Femur of anterior legs much broader than that of other two pairs and equal to or slightly longer than tibia and tarsus together; in middle and posterior legs femur distinctly shorter than corresponding tibia and tarsus together. Tibia and tarsus slender, the separation between them definite but not conspicuous; both segments broadest at junction. Tarsus slightly shorter than tibia, average ratio being 0·95 in anterior legs and 0·87 and 0·80 in middle and posterior legs respectively. Claw (figs. F, G) slightly curved with base projecting ventrally into a short point; claws of anterior legs (F) short and stout, of middle and posterior legs (G) longer and slender. Actual measurements of segments in μ as follows:

	Legs.					
	Anterior.		Middle.		Posterior.	
	Range.	Average.	Range.	Average.	Range.	Average.
Femur: Length	38·5 –42·0	39·0	38·5 –45·5	41·8	42·0 –45·5	44·0
Width	17·5 –24·5	20·0	14·0 –17·5	16·0	14·0 –17·5	15·8
Tibia: Length	17·5 –21·0	19·6	21·0 –26·25	23·45	22·7 –28·0	26·25
Tarsus: Length	17·5 –21·0	18·5	17·5 –22·75	20·55	21·0 –24·5	22·75
Tarsus and Tibia Length	35·0 –40·0	37·5	42·0 –49·0	45·8	47·0 –56·0	51·4
Tarsus and Tibia Width	7·0 –10·5	10·22	7·0 –10·5	8·82	7·0 –10·5	8·40
Ratio:						
Length $\frac{\text{Tarsus}}{\text{Tibia}}$	0·83– 1·00	0·95	0·79– 1·00	0·87	0·75– 0·93	0·80
Claw: Length (approx.)	.	13·0	.	17·0	.	19·0

Each coxa with three small setae, two on anterior and one on posterior face near articulation with trochanter. Trochanter with a single minute seta on anterior face near articulation with coxa and with one long seta on ventral face ; in anterior legs this seta longest both absolutely (about 65μ) and relatively, reaching beyond distal end of tibia, while in middle and posterior legs it is shorter (about 57μ and 52μ respectively), reaching one-half and one-quarter length of tibia respectively. Femur with a single seta (about 6μ long) in middle of anterior face. Tarsus with two setae, one ventrally and one dorsally, at distal end. Each claw with two spatulate digitules about 1·5 length of claw. Tibia without setae. Framework of *mouth parts* comparatively large, arches of tentorium reaching half the distance between anterior and middle coxae and labral apex opposite middle coxae ; close behind lies a one-segmented elliptical labium, 40μ long and 25μ wide, (Bochenska, 1939) (homologies of the mouth parts). *Spiracles* in nine pairs, two thoracic and seven abdominal. Thoracic spiracles (Plate 1, fig. I*a*, *b*) subventral in position and extremely inconspicuous ; trachea opens in centre of a slightly sclerotised disc about 3μ in diameter, which in optical section may be interpreted as a small conical atrium with the trachea arising centrally from the bottom ; surrounding membranous derm folded and disc always appears more or less invaginated. Abdominal spiracles (J) on margins, one pair on each of the seven anterior abdominal segments ; these similar to the thoracic spiracles, but what is interpreted as the atria more distinctly sclerotised, each projecting button-like from bottom of a circular sclerotised cup-like invagination ; the invaginations 7–8μ in diameter and 5μ deep, 15–18μ apart, i.e., about twice diameter of cup. No visible derm pores associated with spiracles, but after settling, a small amount of granular waxy secretion appears on living individuals in area occupied by abdominal spiracles. *Derm vestiture :* Dorsum on each side with a single subdorsal row of minute setae, one on each of (8) abdominal and (3) thoracic segments, and one on head. With the exception of the seta on last abdominal segment, which is slightly longer, the setae comprising row very small (about 4μ long). Posterior end of abdomen with one pair of apical and one pair of subventral setae ; apical setae, 164–200μ long (average 184μ), i.e., about half length of body ; subventral setae shorter, about 35μ long. Venter with single pair of minute setae on last abdominal segment. No *derm pores* present. *Segmentation* distinct, especially on dorsum of abdomen, where it is emphasised by the segmentally arranged spiracles and subdorsal series of setae. *Anal opening* not observed.

b. *The Growing Period.*

During the growing period the size and shape of the larva change considerably. At first an increase in length takes place, and this is followed by an enormous swelling of the cephalothoracic area. Fig. 1, *b*–*f*, shows diagrammatically a reconstructed growth-series, all drawings being made to the same scale from selected specimens at various stages. From the position of the spiracles, legs, labium, and the antennae it is evident that the part most affected lies in front of the first pair of thoracic spiracles, i.e., corresponding with prothorax and head ; the whole of this area becoming considerably enlarged both transversely and longitudinally. The two or three apical abdominal segments remain unchanged, while the anterior abdominal segments, meta- and mesothorax gradually broaden and become continuous with the expanded cephalothorax. The actual shape of a growing or fully grown larva depends on the space available ; in natural conditions, under bark scales or in crevices, the insects are usually distorted, at least considerably flattened and sometimes strangely asymmetrical. There is no intermediate moult at this stage in *M. pini*, as reported in a few other species (Herbert, 1921 ; McKenzie, 1941), and the increase in size is solely the result of a considerable swelling and stretching of the derm of the originally small larva. Mounted preparations of the extremely asymmetrical individuals, one of which is represented in fig. 2, illustrate this point. The figure shows a nearly fully grown larva and the presence of the much coiled, newly developing mouth parts is an obvious sign of an early preparation for the moult. The young larva has placed itself with one side of the body close to the far end of the space under the bark scale and consequently did not expand on this side at all ; here the distances between the legs, antennae

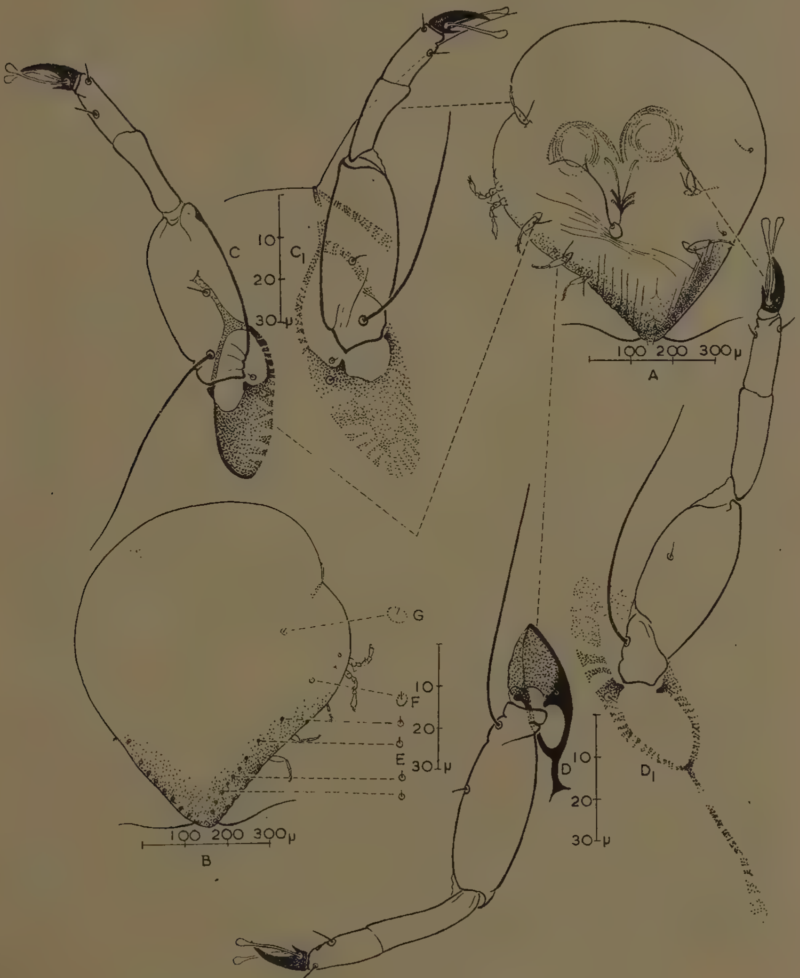

FIG. 2.—1st stage larva, extremely assymetrical specimen. A, ventral ; B, dorsal ; C, C_1, anterior legs and D, D_1, middle legs showing the difference in coxae of not expanded and expanded sides ; E, F, G, setae of the subdorsal row with gradually enlarged bases.

and spiracles correspond closely with that of the young larva. Compensatory swelling and expansion, both in degree and in the area involved, has occurred on the other "free" side of the body. Detailed examination of the preparation reveals that the coxae and the bases of the derm setae are also affected by the stretching. The coxae of the unchanged side (*c*, *d*) are normal, bulging from the body as originally in the young larva, and the basal rims are uniformly sclerotised and well delimited; the coxae on the expanded side of the body (c_1, d_1) are flat, their bases enlarged, the basal sclerotisations divided into small fragments separated by transparent membranous areas, poorly delimited and gradually merging with the surrounding membranous derm. The bases of the derm setae in the stretched areas are enlarged, less conspicuous, or even disappearing (*f*, *g*), The spiracular depressions on the margins of the abdomen remain unchanged.

c. *The Fully Grown* 1*st Stage Larva.*

Body more or less pyriform, anteriorly broadly rounded, posteriorly acute with margins of mid-abdomen concave; usually distorted, the degree depending on the space available; about 2·5 times longer and over three times broader across anterior half of body than newly hatched individuals. Actual dimensions in μ of fully grown 1st stage larvae as follows:

	Length.		Width.		Height.	
	Range.	Average.	Range.	Average.	Range.	Average.
Living individuals .	600–800	730	400–700	550	200–600	398
Mounted individuals	750–850	811	600–770	673	.	.

Colour amber yellow, with posterior end and margins of the abdomen darker. *Derm* in anterior part of body membranous, thin and smooth; on posterior abdominal segments slightly sclerotised and wrinkled; around abdominal spiracles areolate (Plate I, fig. K). *Eye-spots* of reddish-brown colour visible on living specimens but no corresponding cuticular structures to be found on mounted preparations. Small amount of granular waxy secretion in form of a narrow marginal fringe present in area of abdominal spiracles. *Antennae, spiracles, legs,* and *derm vestiture* as in young larva, their relative positions being different due to the swelling of the anterior part of the body. Coxae, especially those of anterior legs, flat, not bulging as normally, and with bases enlarged and feebly delimited. Bases of derm setae in the stretched area enlarged and often difficult to locate.

d. *Method of Moulting.*

At moulting the skin breaks anteriorly and splits longitudinally in the median dorsoventral plane. Apparently there is no fixed point for the initial break; it is possible that the skin breaks at the most stretched and thinnest place, usually somewhere between the base of the antenna and the base of the anterior coxa on one or other side. The cast skin therefore usually bears both antennae and three legs on one side of the rupture and three legs only on the other. Occasionally the break occurs between the anterior and middle coxae. During the growth of the ensuing stage the larval skin gradually slips sideways and backwards; it remains however in an equatorial plane encircling the posterior half of the body of the intermediate stage.

3. The intermediate stage (Plate II, figs. A–G).

a. *Description.*

Body stout ovoid, rounded anteriorly and broadly rounded posteriorly; owing to the pressure of the surrounding plant tissues and the limited space usually flattened and more or less distorted. When exposed, living specimens assume ovoid shape, narrowed and somewhat conical anteriorly and broadened posteriorly. Mounted specimens (fig. A) stout, elliptical to circular. Comparatively small at eclosion, almost double their linear dimensions at maturity. Actual measurements in μ as follows :

	Length.		Width.		Height.	
	Range.	Average.	Range.	Average.	Range.	Average.
Not mounted :						
At eclosion	700– 910	800	600– 700	647	140–650	383
At maturity	1050–1890	1526	910–1680	1122	210–840	486
Mounted :						
At eclosion	730–1250	970	660–1100	856	.	
At maturity	1200–2100	1639	1000–1820	1410	.	.

As indicated by the position of the spiracles and labium the whole body is uniformly and equally affected by the growth. *Colour* at first amber yellow ; at maturity greyish-yellow with darker margins. *Derm* at eclosion soft and membranous ; later hard, thin and homogeneous, more or less sclerotized especially on margins around the spiracles ; surface smooth, entirely without pattern. *Antennae* and *legs* entirely wanting. Dark *eye-spots* visible on living specimens but without corresponding cuticular structures on mounted preparations. Framework of *mouth parts* anterior to centre of body, relatively large. Labium one-segmented, central in position and apparently perpendicular to surface of body ; compressed antero-posteriorly and in mounts, usually distorted ; in frontal view (fig. B) somewhat resembling that of 1st stage larva but much larger, 70–98μ long and 49–59μ wide ; in the commonly occurring distorted condition (fig. A, *b*) much wider (84–101μ) and about 42μ high, the latter probably also representing a distorted condition. *Spiracles* subventral in position, the two thoracic pairs being slightly more median than the seven abdominal. All are alike ; each with opening of trachea situated within a tubular depression slanting anteriorly at an acute angle (about 40–50°) to surface of body, the angles more acute (40°) in posterior abdominal spiracles ; inner end of depression closed by a conspicuous pore plate. In young individuals depressions only slightly sclerotised ; at maturity and on cast skins sclerotisation very heavy, and, viewed from outside the pore plate, apparently surrounded by a thick sclerotised band or ring (fig. 3, *c*). Pore plates (figs. C -F) somewhat pedicellate, convex, with small pores (2–3μ in diameter) slanting through plate towards centre. Thoracic spiracles largest, the abdominal smaller, decreasing in size posteriorly, the last (7th) being usually smallest (Plate II, figs. C–F). Relations between various structures of the spiracles fairly constant. Both diameter and depth of external opening of each invagination, as measured along the longest (posterior) side, about 1·1–1·25 times diameter of corresponding pore plate ; depth of depression along shortest (anterior) side only half diameter of pore plate. More numerous pores in larger plates, size of pore being independent of plate size. Actual figures of structural details as follows :

Spiracles :	Pore plates.				Depth of the depressions (longest side). Averages of 2–6 readings in μ.	Pore plates of the specimen 164*a*.	
	Diameter in μ.		Number of loculi.			Diameter in μ.	Number of loculi.
	Range.	Average.	Range.	Average.			
Thoracic :							
Ist	15·8–24·5	19·1	19–28	23·0	23·4	19·3	20
IInd	15·8–24·5	18·6	15–25	19·3	23·3	17·5	16
Abdominal :							
1st	14·0–17·5	15·0	12–21	16·0	18·0	15·8	12
2nd	12·2–17·5	13·9	8–18	13·7	17·8	12·3	8
3rd	10·5–17·5	13·1	9–15	11·2	14·0	14·0	10
4th	9·8–15·8	12·2	7–16	10·4	14·4	12·3	8
5th	8·7–15·7	11·5	7–13	10·1	13·4	12·3	7
6th	8·7–12·2	10·3	6–13	9·0	11·3	10·5	7
7th	7·0–12·2	9·05	5–13	7·2	10·0	7·0	5

The trachea of the thoracic spiracles enters the morphologically median side near the bottom of the invagination (figs. C, D) ; that of the abdominal spiracles, at the bottom of the invagination morphologically posterior to the pore plate. Sometimes the pore plate of the posterior abdominal spiracles is cleft for the reception of the opening of the trachea (fig. F). From the small opening (2–3μ in diameter) the trachea of each spiracle runs radially towards the centre of the body widening gradually, and in a distance of about two to three times the diameter of the corresponding pore-plate divides into a bunch of small tracheae. There are no derm pores and no derm vestiture. At the posterior apex in the middle line subventrally there is a sclerotised structure appearing like a longitudinal suture with the rudiments of two openings (fig. G). This structure is

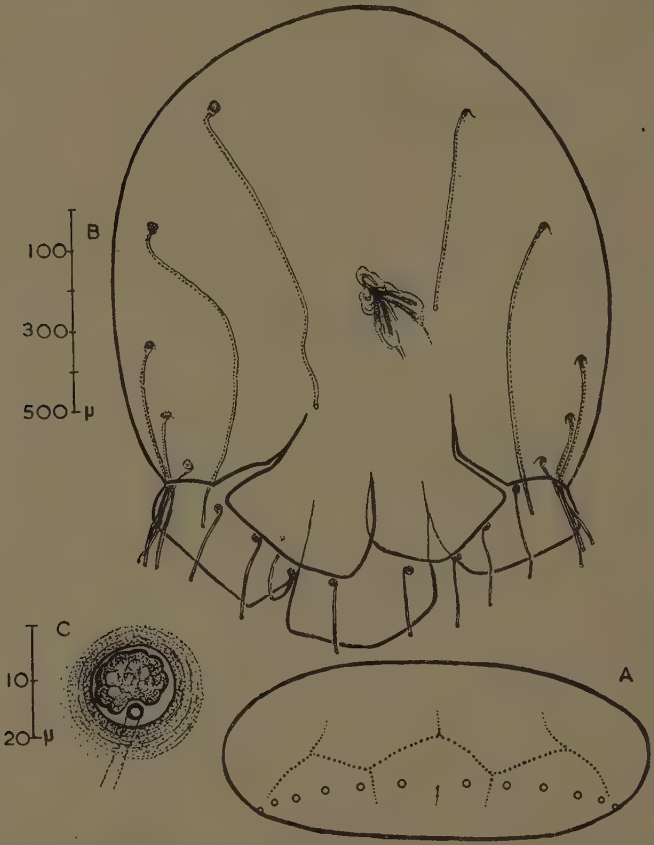

Fig. 3.—Intermediate stage. A, posterior view showing prospective ecdysial lines (diagrammatic) ; B, cast skin ; C, 6th abdominal spiracle in surface view as it appears in fully grown individuals and on cast skins.

entirely superficial and is not visible in young specimens, but detectable on well-stained preparations of fully grown specimens and on the cast skins. As observed in moulting individuals, its position corresponds with that of the posterior cleft, at the bottom of which opens the genital opening of the adult female.

b. *Method of Moulting.*

The moulting pattern is constant and characteristic. Fig. 3*a* represents diagrammatically the posterior view of this stage, with dots indicating approxmately the prospective ecdysial lines. The skin breaks along a somewhat zig-zag horizontal line (*t–t*) extending subdorsally along the posterior margin of the body towards the vicinity of the third abdominal spiracle on each side, and then along five more or less longitudinal lines (*l, l, l, l, l,*) running anteriorly from the apices of the turning points of the zig-zag line. As a result the skin splits into five flaps (fig. 3*b*), two dorsal and three ventral, forming the opening through which the adult female escapes. The median ventral flap always bears the last (7th) pair of abdominal spiracles, while each of the lateral ventral flaps bears the 4th, 5th and 6th spiracles of the corresponding side. The regularity of this pattern is often obscured in distorted individuals.

It should be emphasised that, unlike *Steingelia gorodetskia* Nass., the other British Margarodid, in which the ecdysial lines (of quite a different pattern) are distinct throughout the whole life of the corresponding intermediate stages (unpublished observation), in *M. pini* these lines are not visible even in fully grown individuals, until the actual splitting occurs.

4. The adult female (Plates III and IV).

a. *Description.*

Body soft and highly flexible ; in motion its shape and dimensions change considerably ; at rest the body is contracted and somewhat rolled up like a hedgehog. "Normal" size and shape can be estimated fairly accurately from the average of several measurements of the steadily moving insect placed under a binocular microscope on $\frac{1}{10}$ cm. graph paper. It is then seen to be elongate, nearly parallel-sided, narrow ; about 3·5 times longer than wide. Anterior end flattened and tapering towards bases of antennae ; abdomen almost round in cross-section, slightly swollen posteriorly, and with a shallow vertical notch at broadly rounded apex. Actual dimensions vary individually ; length from 2·2 to 3·9 mm. ; width from 0·8 to 1·1 mm. Mounted specimens (Plate III, fig. A) about 10–20 per cent. longer and 30–40 per cent. broader, thus elongated and broadest at the middle of the abdomen ; length 2·6–4·45 mm. (Type 3·5 and 4·1 mm.) ; greatest width 1·0–1·85 mm. (Type 1·4 and 1·5 mm.). Anterior end tapering gradually towards bases of antennae ; posterior end broadly rounded with apical notch more or less obscured. *Derm* apparently composed of two partially separated cuticles ; both membranous ; the external very thin and showing a faint "shagreen pattern" (Green, 1925), internal without pattern. At the more sclerotised parts (sclerotised segments of legs and antennae, basal rings of derm setae, at opening of derm pores), both cuticles fused, but distinctly separated elsewhere, even inside atria of spiracles (Plate IV, figs. G, H, I, J). This seems to be a true partial separation and not an artefact due to mounting technique. Living insects exhibit a characteristic opaque shine on surface of body, and edges of folds formed during movements are fringed with narrow whitish rims ; patches of external cuticle can be brushed off, with difficulty, from living specimens which do not survive the treatment, more easily from specimens preserved in alcohol, and quite easily from individuals treated with potash.

On mounted specimens the external cuticle is as a rule damaged, fragmented, or partially missing—as may be seen on the specimens of the Type slide. *Antennae* (Plate IV, fig. A) nine-segmented, situated at anterior end of body ; approximate distance between bases about half width of basal segment ; length 421–586μ (average 512μ ; Type 450 and 580μ), i.e., one-seventh length of body. The first two segments taper distally, the 1st being 112–161μ broad at base (average 140·5μ). Segments 3 to 9 uniformly slender, greatest width of each being about 50μ ; 3rd segment cylindrical, 4th to 8th broadest distally, and 9th ovoid with truncate apex. Absolute and relative length of segments vary considerably, the only constant feature being that the 1st segment is the longest and the 3rd the shortest. Averages and ranges of lengths of segments in μ as follows :

	Segments.								
	1st.	2nd.	3rd.	4th.	5th.	6th.	7th.	8th.	9th.
Average	116·0	59·0	39·5	49·0	49·0	50·0	49·5	50·0	59·0
Range	88–140	45–70	35–46	35–57	35–57	38–57	35–57	38–57	46–63

From the above it would appear that segments 4 to 8 are subequal and, indeed, in some individuals this is so ; in others, however, any of these five segments may be the longest or the shortest. 1st and 2nd segments imperfectly sclerotised and wrinkled longitudinally ; 3rd to 9th sclerotised with a transverse scaly pattern (transversely rugose, Green, 1925). 1st segment bears a group of 7 to 10 minute setae (about 5μ long) at base dorsally, and an incomplete band of 15 to 23 larger setae (8–10μ long) across middle part of segment ; 2nd segment with a similar band of 8 to 13 setae of variable length (10–25μ), and among those 3 to 5 round sensoria on dorsal face of segment ; segments 3 to 9 each bear distally a circle of slender setae (12–25μ long), there being 6 to 8 setae on 3rd segment, 4 to 5 on segments 4 to 8, and 5 on 9th. Setae on ventral face of segments longest. Apart from the setae, segments 6 to 9 each bear ventrally a pair of stout curved spines, 16–19μ long and about 4μ broad at their base. Occasionally one similar but smaller spine (about 10μ long) on 5th segment (Plate IV, fig. B), usually on only one antenna.[2] Within the cuticle of median side of segments 5, 6 and 7 a pair of short pointed sclerotised struts (Plate IV, fig. B, *s*), similar to those of the 1st stage larva, but comparatively shorter and stouter. *Eyes* small but distinct, situated on margins behind antennae ; surrounding derm irregularly sclerotised. *Mouth parts* entirely absent, position of mouth being indicated by a very much folded longitudinal funnel-shaped depression. *Legs* (Plate IV, figs. C, D, E) well developed. Coxa of normal shape, comparatively large, imperfectly sclerotised and therefore often distorted on mounts. Femur of anterior legs oval, of middle and posterior legs broadest at base and tapering distally ; well sclerotised, especially the dorsal and distal portions ; length approximately one-third total length of leg, and greatest width slightly less than half the length. Tibia well sclerotised, subequal in length to femur, but slender, its greatest width about one-quarter of length ; in side view tibia appears bowed, ventral margin being straight and almost continuous with oblique proximal end, while dorsal margin is convex. Tarsus two-segmented ; first segment short, membranous and transversely wrinkled ; second segment longer and well sclerotised ; the two tarsal segments together shorter than tibia (about two-thirds length of tibia). Claws short, about one-half length of second tarsal segment ; stout and falcate with small pointed projection at base. Sclerotised parts of femur, tibia, and tarsus with a distinct transverse

[2] In his original description E. E. Green has stated (p. 34) of the segments, " 5th to 9th each with two stout curved spines and a few shorter setae." Examination of Green's specimens revealed that none shows two spines on the 5th segment. One specimen on the Type slide has one small spine on the 5th segment of only one antenna ; the second Type specimen, as well as the specimens on the other three slides, show no spines on the 5th segment at all. Fifty specimens were examined from my collection and none was found bearing 2 spines on the 5th segment ; one small spine on this segment was found in 7 individuals, i.e., 14 per cent., but even then always in only one antenna.

scaly pattern similar to that of the antennal segments. Anterior legs shortest, the middle and posterior pairs becoming gradually longer, ratio being 1·00:1·16:1·22. Length of legs in μ (as a sum of the individual measurements of sclerotised segments, i.e., femur, tibia, second tarsal segment, and claw) as follows :

	Legs.					
	Anterior.		Middle.		Posterior.	
	Range.	Average.	Range.	Average.	Range.	Average.
20 specimens examined :	366–544	478·9	429–626	555·0	411–696	583·7
Type specimens :	538		610		644	
	540		606		648	

Each coxa with a group of 8–12 minute setae (about 5μ long) on both anterior and posterior faces. Trochanter with 3 to 4 sensoria, and two setae (8–15μ long) on each side near articulation with coxa ; ventral face of distal part of trochanter usually with one long seta, length of which varies from 49 to 79μ, normally longest on the anterior legs (71μ), and shorter on middle (66μ) and posterior (63μ) legs. Occasionally two setae on trochanter (Plate IV, fig. F), the additional second seta being much shorter (21–42μ long) and occurring irregularly on one or two, rarely on three or four legs of an individual.[3] On mounts both setae are often broken off, but remaining basal discs show the actual condition. Setae on femur small (10–15μ long), arranged in irregular rows on dorsal and lateral sides. On tibia setae arranged similarly, but more crowded on distal half, there forming two conspicuous rows along inner margin and an apical cluster of larger setae (25–30μ long). No setae on first tarsal segment ; second (sclerotised) with a group of 3–4 setae (about 20μ long) on each side proximally, two more or less distinct rows along inner margin, and a few similar setae in a circle at distal end. Claw with a pair of spatulate digitules of about 1·3 length of claw. Nine pairs of *spiracles*, two thoracic and seven abdominal, the latter on 2nd to 8th abdominal segments. All spiracles subventral in position and similar in structure (Plate IV, figs. G–J) ; the irregular external opening leads into a globular atrium with the opening of the trachea in the centre of the slightly inflated bottom. Thoracic spiracles largest and abdominal smaller, decreasing in size posteriorly. Diameter of the atria (in μ) are as follows :

	Spiracles.							
	Thoracic.				Abdominal.			
	Ist.		IInd.		1st.		7th.	
	Range.	Average.	Range.	Average.	Range.	Average.	Range.	Average.
20 specimens	19·0–26·0	22·4	19·0–24·5	21·35	10·5–14·0	11·85	7·0–9·5	7·9
Type specimen	26·0		22·5		11·4		7·6	
	26·0		23·0		11·0		7·6	

---

[3] E. E. Green (1925) says (p. 35) that there is " one long seta and one short seta on the trochanter," but none of his specimens show this condition in all the legs. One specimen of the Type slide shows this condition in one anterior leg ; the second Type specimen, in one anterior and one posterior leg. The specimens on the other three slides, as far as it is possible to see, show only one seta on the trochanter of all the legs. Among 50 specimens examined from my collection none was found with two setae on the trochanter of all six legs ; 19 individuals (i.e., 38 per cent.) were found with one long and one shorter setae on the trochanter, usually on one or two legs, and only two showed this condition on the trochanter of three and four legs respectively.

Trachea of each thoracic spiracle comparatively wide ; of the abdominal spiracles narrower, but all approximately of the same length (30–35μ) ; internally trachea ends in a crowded tuft of fine tracheal tubules ; walls of tracheae of thoracic spiracles show faint reticulation (Plate IV, fig. G). The separated and much folded external cuticle is clearly visible inside the atrium of each spiracle. *Bilocular derm* pores are distributed all over surface of body ; on abdomen and on dorsal aspect of thorax they are arranged in more or less complete rows alternating with short marginal rows or clusters, one of each of these on each segment ; on prothorax and head this arrangement somewhat irregular and the rows obscured (Plate III, fig. A). First abdominal row behind posterior coxae, which extends across the dorsum and margins but is missing in mid-ventral area, composed of 21 to 28 pores (average 23·0 ; Type 21 and 23 pores) ; second transverse abdominal row complete and composed of 25 to 35 pores (average 30·0 ; Type 25 and 32 pores). On ventral aspect of thorax bilocular derm pores occur in small groups of 2 to 4 in front of each coxa. Pores on both ventral and dorsal surfaces of body of same size and structure. Disc convex, 7·6–10·6μ in diameter (average 8·6μ) ; central duct subequal in length to diameter of disc, bilocular, with inner end slightly enlarged. On dorsal side of head and thorax discs deeply invaginated (Plate III, fig. B), and there the bilocular centre of the disc is connected by a simple membranous tube with the irregular opening on the surface of the body ; elsewhere discs much less invaginated or not at all. *Multilocular derm pores* in a cluster of 30 to 37 (average 34 ; Type 34 and 37 pores) within and around apical cleft at posterior end of abdomen. The disc of these pores, 8·7–10·5μ in diameter (average 9·4μ), is shaped like an inverted cup with slightly inflated base (Plate III, fig. D) ; central duct short (about half the diameter of the disc), usually bilocular, sometimes trilocular, opens at bottom of invaginated centre, and the peripheral loculi, 10–12 (average 10·6) to the pore, opening in the sloping sides. *Body setae* are associated with the bilocular derm pores and arranged in similar rows and clusters ; generally small (Plate III, figs. E, F, G, J, K, L), the smallest (3·5–5·7μ long) being those on the margins of the body (F), slightly longer ones (5·2–8·0μ long) on dorsum (L), and still longer (5·7–12·0μ) on the head (E) and the posterior apex (K). On ventral side of the abdomen setae near median line much longer, the longest being 27–38μ (average 31·8 ; Type 30·0 and 38·0μ), with the smallest seta in the same row 5·2–7·0μ long (J). On ventral side of thorax setae arranged in precoxal and intercoxal groups. The former groups (Plate III, fig. H), one in front of each coxa, well defined and composed of a variable number of 2 to 6 small setae (5·7–7·6μ long). The latter groups (Plate III, fig. I) scattered over median and medio-posterior area in relation to each coxa ; number of setae in each group varies from 3 to 8 and length varies considerably from the smallest, about 7μ long, to the largest, up to 41μ long, in the same group. *Dorsal cicatrices* (Morrison, 1939) (callosities, E. E. Green, 1925 ; simple pores, Herbert, 1919, 1921 ; Morrison, 1928) occur on median part of dorsum forming five transverse bands, one on each of 3rd to 7th abdominal segments (Plate III, fig. A) ; bands on segments 4 to 6 wide and occupy whole length of segment ; bands on segments 3 and 7 incomplete, the former often reduced to a single row near posterior margin of segment, and the latter to a few cicatrices scattered in middle of segment ; total number of cicatrices varies from 202 to 334 (average 282 ; Type 288 and 295). Cicatrices (Plate III, fig. L) irregularly rounded, 4·2–9·5μ in diameter (average 6·5μ). *Genital opening* situated at bottom of the posterior cleft ; usually obscured by folds of the derm, but some specimens which have been mounted after or during the process of oviposition show the apical cleft wide open and the genital opening exposed. *Anal opening* not observed.

b. *Comparison of the Females of the Two Generations.*

The females of the two generations differ in the average size of the body and in the averages of some other metrical and numerical characters. The means are higher for the spring generation, although the ranges of both generations overlap considerably. Range of the length of the body in two samples, $N_1 = 30$

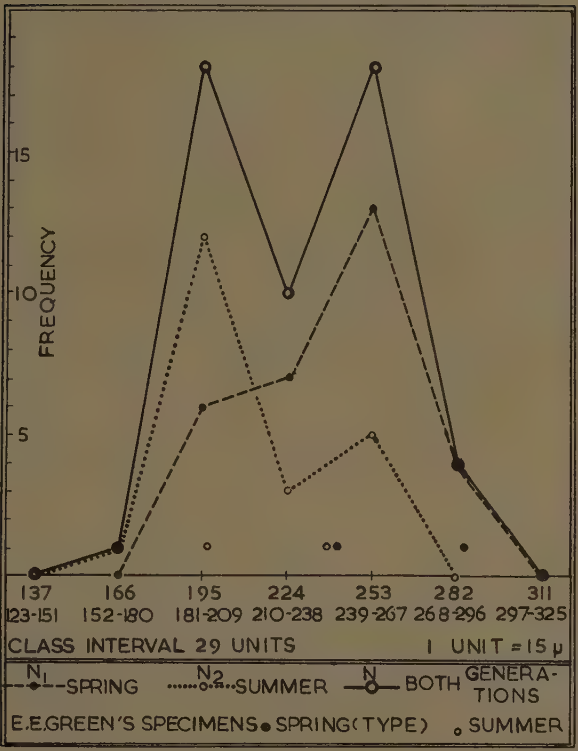

FIG. 4.—Frequency polygons; distribution of the length of the body of adult females of spring, summer, and both generations.

STATISTICS.

Summer Generation.

$N_2 = 21.$
$M_2 = 214{\cdot}0 \pm 6{\cdot}13 (= 3{\cdot}21 \pm 0{\cdot}091 \text{ mm.}).$
$\sigma_2 = 28{\cdot}2 \pm 3{\cdot}64 (= 0{\cdot}419 \pm 0{\cdot}042 \text{ mm.}).$
$R_{2 \text{ obs.}} = 174\text{–}265 \ (= 2{\cdot}61 - 3{\cdot}95 \text{ mm.}).$
$V_2 = 13{\cdot}1.$

Spring Generation.

$N_1 = 30.$
$M_1 = 239{\cdot}1 \pm 5{\cdot}32 (= 3{\cdot}54 \pm 0{\cdot}081 \text{ mm.}).$
$\sigma_1 = 29{\cdot}2 \pm 3{\cdot}93 (= 0{\cdot}448 \pm 0{\cdot}057 \text{ mm.}).$
$R_{1 \text{ obs.}} = 185\text{–}295 (= 2{\cdot}77 - 4{\cdot}45 \text{ mm.}).$
$V_1 = 12{\cdot}2.$

$$t = \frac{\bar{x} - \bar{x}'}{s}\sqrt{\frac{(n_1+1)(n_2+1)}{n_1+n_2+2}} = 3{\cdot}05\,; \quad \frac{d}{\sigma_d} = \sqrt{\frac{M_1 - M_2}{\frac{N_1}{N_2}s^2{}_{M_1} + \frac{N_2}{N_1}s^2{}_{M_2}}} = 5{\cdot}7$$

$P =$ less than $0{\cdot}01.$

Both Generations.

$N = N_1 + N_2 = 51.$
$M = 228{\cdot}7 \pm 4{\cdot}30 (= 3{\cdot}42 \pm 0{\cdot}065 \text{ mm.}).$
$\sigma = 31{\cdot}1 \pm 3{\cdot}50 (= 0{\cdot}465 \pm 0{\cdot}052 \text{ mm.}).$
$R_{\text{obs.}} = 174\text{–}295 (= 2{\cdot}61\text{–}4{\cdot}45 \text{ mm.}).$
$V = 13{\cdot}7.$

specimens of the spring generation, and $N_2 = 21$ specimens of the summer generation (all collected in 1949) is represented in fig. 4. The frequency polygon of the two samples together $(N_1 + N_2)$ is bimodal ; the polygons of each sample separately appear to be mirror-images of each other, although the second (N_2) is irregular, probably due to the smaller number of specimens in the sample. Both samples reveal rather high values of the coefficient of variation ($V = 12{\cdot}2$ and $13{\cdot}1$ respectively) ; the mean body length of the females of the spring generation is much higher and comparison of the two means, by calculating $t = 3{\cdot}05$ and $d/\sigma_d = 5{\cdot}7$, both of which correspond with the value of $P = <0{\cdot}001$, shows that the difference is highly significant. It may be noted that the respective positions of Green's original specimens are indicated in the diagram by appropriate dots, and that they fit well within the ranges of their respective generations.

Ten specimens of each generation selected at random from the best mounts have been examined in detail. The characters studied fall into three groups :

I. Characters which show higher mean values in the spring generation.

	Spring generation.		Summer generation.	
	Range.	Average.	Range.	Average.
1. *Body* (in mm.) :				
Length . . .	2·80–4·40	3·78	2·63–3·45	3·05
Width . . .	1·12–1·75	1·43	1·16–1·56	1·27
2. *Antennae* (in μ) :				
Total length . .	506–586	543·2	421–543	481·0
Width at base . .	141–161	152·0	112–148	129·0
Width of the 9th segment	46–52	50·0	35–42	38·0
3. *Legs* :—Total length (sum of the sclerotised segments) (in μ) :				
Anterior leg . .	422–544	505·2	366–511	452·3
Middle leg . . .	471–626	587·0	429–593	523·5
Posterior leg . .	513–696	623·7	411–696	583·75
Length of the long seta on trochanter (in μ) :				
Anterior leg . .	69–79	74·0	49–70	62·4
Middle leg . . .	58–76	68·0	49–74	63·0
Posterior leg . .	58–76	66·6	49–76	58·0
4. *Body setae* :—Length (in μ) :				
Largest midventral seta	28·0–38·0	33·6	28·0–35·0	30·0
Intercoxal setae . .	9·5–41·0	28·5	7·0–35·0	24·1
5. *Dorsal cicatrices* :				
Total number . .	250–334	304·0	202–316	264·2

II. Characters which show the same or approximately the same ranges and mean values in both generations.

	Spring generation.		Summer generation.	
	Range.	Average.	Range.	Average.
1. *Spiracles* :—Diameter of atrium (in μ) :				
1st thoracic	19·0–26·0	22·7	21·0–24·5	22·1
1st abdominal	11·4–13·0	11·8	10·5–14·0	11·9
7th abdominal	7·6–9·5	8·0	7·5–9·5	7·8
2. *Bilocular derm pores* :—Number in :				
1st abdominal row	21–26	22·5	21–28	23·4
2nd abdominal row	25–34	29·3	26–35	29·6
Diameter of the disc (in μ)	7·6–10·6	8·6	7·6–10·2	8·6
3. *Multilocular derm pores :*				
Total number	30–37	33·7	33–37	34·0
Diameter of the disc (in μ)	8·7–10·5	9·3	8·7–10·5	9·5
Number of loculi	10–12	10·5	10–12	10·8
4. *Dorsal cicatrices :*				
Diameter (in μ)	4·2–9·5	6·7	5·2–7·7	6·4

III. Characters which do not show consistent differences in their mean values in the two generations.

1. Number of setae in pre- and intercoxal groups (the inconsistency is probably due to high variability—coefficient of variation $V = 25$–27),
2. Length of the small body setae (the inconsistency may have resulted from the measurement error due to the small size of the setae and variable orientation on mounts).

Some of the characters from all three groups have been suggested and used for characterisation of the species within the genus. As far as *Matsucoccus pini* is concerned, the three groups suggest that the characters in each, taken as they are, should have different taxonomic values ; for instance, Group I suggests correlation of the characters with the size of the body.

c. *Statistical Analysis of the Variability of Certain Characters.*

Having at hand a certain amount of homogeneous material (from the same locality, practically all from the same host tree, and collected during the same season), further statistical analysis has been undertaken to determine the relations of the characters to the size of the body and their minimum variability as exhibited by the two generations of the same population. For this purpose seven specimens of each generation have been selected at random and treated together as one sample of $N = 14$ specimens ; thus most calculations are based on 14 observations or 14 pairs of observations. It is fully realised that this number is rather low, but the following points may perhaps justify recording and discussing the results obtained :

1. Coccoidea, in general, are technically very difficult material for measurement, and perfect material essential for the purpose is not often available in quantities even as large as the above.

2. The sample is apparently random, there being three factors responsible for this, namely : thorough collecting, subsequent elimination of a large number of specimens during mounting due to distortion, and then actual selection from the best mounts.

3. Similar characters (setae, or derm pores) and homodynamous organs (legs) give consistent results, although for some slightly different sets of specimens have been used.

4. Some of the results obtained support the views already arrived at by workers in other groups of Coccoidea.

5. Since the basis for specific characterisation within the genus is not established, the analysis may provide some indications as to the taxonomic value of the various characters.

The following characters have been studied and their statistics calculated :

	N.	M. $\pm\sigma_M$.	σ. $\pm\sigma_\sigma$.	R_{obs}.	*V*.	$r_{y,x}$.	*t*.	P.
Group I.								
Antennae :								
Length (y_1).	14	514·70 13·45	50·40 9·52	421–586	9·80	0·736	3·730	<0·01
Legs : Length—								
Anterior (y_2)	13	483·40 15·42	57·50 10·87	366–544	11·90	0·724	3·475	<0·01
Middle (y_3) .	14	521·50 15·62	58·50 11·04	397–586	11·35	0·945	10·10	<0·001
Posterior (y_4)	13	582·25 20·79	77·5 14·65	411–696	13·30	0·911	7·01	<0·001
Ventral setae :								
Length (y_5).	14	32·5 1·08	4·03 ·762	28–38	12·5	0·619	2·74	0·01–0·02
Dorsal cicatrices.								
Number (y_6)	14	281·3 10·26	38·4 9·07	202–334	13·7	0·712	3·53	<0·01
Group II.								
Derm pores :								
Multilocular : Total number	14	34·0 ·56	2·09 ·395	30–37	6·15	0·224	0·797	0·5–0·6
Bilocular :								
Number in—								
1st abdominal row	14	23·0 ·601	2·25 ·425	21–28	9·77	0·339	1·245	0·2–0·4
2nd abdominal row	14	28·57 ·876	3·28 ·620	24–35	11·6	0·508	1·04	0·05–0·1

In group II the selected characters show slightly lower values of the coefficient of variation, and no significant correlation with the length of the body (x). This, if confirmed in a larger sample, would indicate that these characters, being comparatively constant and independent of the size of the insect, may be successfully used for characterisation of *M. pini* and perhaps of the other species of the genus. The other characters of Group II may well be of the same taxonomic importance, though no statistical analysis has been made.

The characters of Group I show rather higher values of the coefficient of variation, and all show significant positive correlation with the length of the body. The consistency of these results is remarkable as, even in the best mounts, small distortions of the flexible body and of the organs are unavoidable.

In order to determine the nature of the correlation, further analysis has been applied to the total length of the antenna (y_1), the total length of the middle legs (y_3), and to the total number of dorsal cicatrices (y_6). The statistics of the ratio $\left(\frac{y}{x}\right)$ of these characters (y) to the length of the body (x) have been calculated.

N = 14.	M.	σ.	$R_{obs.}$	V.	$r_{\left(\frac{y}{x}\right), x}$	t.	P.
$\frac{\text{Ant. length}}{\text{Body length}}$	0·146	0·0166	0·166–0·118	11·35	−0·865	5·98	<0·001
$\frac{\text{Leg length}}{\text{Body length}}$	0·158	0·0123	0·175–0·143	13·58	−0·934	8·24	<0·001
Dors. cicatrices:							
$\frac{\text{Total number}}{\text{Body length}}$	82·94	10·75	103·3–68·4	13·0	−0·625	2·77	0·01–0·02

These ratios are smaller in larger insects and all show significant negative correlation with the length of the body. This means that, although the absolute length of the antennae and of the legs and the total number of dorsal cicatrices increase with the increasing size of the insect, the corresponding relative values become smaller, thus demonstrating negative heterogonic growth (Huxley, 1932; allometric growth, Wigglesworth, 1951). The constants (k) of differential (heterogonic) growth and the formulae of both the heterogonic growth ($y = bx^k$) and the rectilinear regression ($y = bx + a$) have been found to be:

	Antennae.	Legs (middle).	Dorsal cicatrices.
k . .	0·447	0·639	0·563
$y = bx^k$.	$y_1 = 13{\cdot}3x^{0.447}$	$y_3 = 3{\cdot}016x^{0.639}$	$y_9 = 140{\cdot}4x^{0.563}$
$y = bx + a$	$y_1 = 0{\cdot}0598x + 301{\cdot}2$ (x and y in μ)	$y_3 = 0{\cdot}0972x + 212{\cdot}9$ (x and y in μ)	$y_9 = 43{\cdot}75x + 131$ (x in mm.)

Comparison of the two formulae (by actual calculation of the corresponding values of y's and summing up the differences between these and y's observed) indicates that the curvilinear form ($y = bx^k$) accords better with the observed data. The anterior and posterior legs behave similarly, and the other characters of Group I, though not analysed statistically, may also well be of a heterogonic nature and their taxonomic value therefore correspondingly limited.

Having available material already measured and partly worked out from the previous calculations, opportunity was taken to carry out an additional analysis to determine the relations of the particular segments of the antenna and of the legs.

Antennae.—The absolute and relative length of the particular segments of the antenna exhibit great variability. The absolute length of each segment is positively correlated with the total length of the antenna and, with the exception of the 2nd segment, the correlation is significant ($P = <0{\cdot}01$) ; the 2nd segment is imperfectly sclerotised and it may be a measurement error, together with the small number of observations in the sample, which result in a non-significant value of the correlation coefficient for this segment. The variability of the relative length of the particular segments is reflected in the great variability of the " antennal formula." The constants of differential growth (k) of the segments calculated in relation to both the total length of the antenna and the length of the body appeared to be different in each segment :

<table>
<tr><th></th><th colspan="9">Segments.</th></tr>
<tr><th></th><th>1st.</th><th>2nd.</th><th>3rd.</th><th>4th.</th><th>5th.</th><th>6th.</th><th>7th.</th><th>8th.</th><th>9th.</th></tr>
<tr><td>k In relation to body length</td><td>0·522</td><td>0·311</td><td>0·433</td><td>0·227</td><td>0·627</td><td>0·558</td><td>0·651</td><td>0·532</td><td>0·366</td></tr>
<tr><td></td><td></td><td></td><td colspan="2">0·419</td><td></td><td></td><td></td><td>0·514</td><td></td></tr>
<tr><td>k In relation to antenna length</td><td>1·071</td><td>0·255</td><td>0·835</td><td>0·736</td><td>1·212</td><td>1·137</td><td>1·318</td><td>1·172</td><td>0·872</td></tr>
<tr><td></td><td></td><td></td><td colspan="2">0·945</td><td></td><td></td><td></td><td>1·065</td><td></td></tr>
</table>

In relation to the length of the body all segments are negatively heterogonic (figs. 5, *a*, *B*-*B*), conforming with the marked negative heterogony of the whole antenna (*b*-*b*). In relation to the total length of the antenna (represented by the line $k = 1$) the 1st, 5th, 6th, 7th and 8th segments are positively heterogonic, while the 2nd, 3rd, 4th and 9th segments are negatively heterogonic (*A*-*A*). There is some irregularity in the values of k for the 2nd segment, which is probably due, as already mentioned, to a measurement error. The centre of differential growth of the antenna lies in the 7th segment ; distally the gradient decreases to a negative value of k in the 9th segment, and proximally gradually smaller " centres " are to be seen in the 5th and 3rd segments separated by the depressions in the 6th and 4th segments. The gradient rises again to a positive value of k in the 1st segment. The length of the first six segments and the length of the last three segments together reveal comparatively small differences in their degrees of differential growth, as the contributions of the component segments tend to cancel each other out ($a_1 - a_1$; $b_1 - b_1$).

The above results have some bearing on the value of the "antennal formula ", very popular at an earlier time, and much relied upon for separation of the species in various groups of Coccoidea. In some cases more recently it has been found unreliable in practice (Ferris, 1918), and therefore its general use abandoned. The various degrees of heterogony of the particular segments in the antenna of *M. pini*, reflected in the great variability of the " antennal formula," seem to support this view, and in this case the formula has no taxonomic value whatsoever. It appears that in species such as *M. pini*, in which differences in length of the particular segments are comparatively small, the various degrees of heterogony of the segments would reveal themselves immediately in a variable antennal formula. In species in which the lengths of the segments differ to a degree which cannot be cancelled out by differences in their heterogony, the antennal formula may still have some value, though perhaps not as a reliable character for specific separation.

Legs (exemplified by the middle pair).—Here, as in previous calculations, only the well sclerotised segments (femur, tibia, 2nd tarsal segment and the claw) have been taken into consideration and related to the length of the body and to the sum of these four segments, called here the total length of the leg. The absolute length of each segment varies considerably, all segments showing significant positive correlation with the length of the body and, except the claw, also with the total length of the leg. The corresponding values of the coefficient of correlation r (and t and P) are as follows :

	The absolute length of—			
	Femur.	Tibia.	2nd tarsal segment.	Claw.
In relation to the length of the body : r . . .	0·913	0·935	0·846	0·776
t . . .	7·7	9·27	5·49	4·25
P . . .	< 0·01	< 0·01	<0·01	<0·01
In relation the total length of the leg : r . . .	0·986	0·991	0·945	0·246
t . . .	19·7	24·3	9·85	0·88
P . . .	< 0·01	< 0·01	<0·01	0·1–0·5

With regard to the relative length of the segments, expressed as a ratio absolute length of the segment/total length of the leg, each segment shows a different relation to the total length of the leg. With the increasing length of the leg this ratio becomes larger for the femur ; for the tibia it remains comparatively constant, and for the second tarsal segment and for the claw smaller. The same relations are shown by the values of both the correlation coefficient (r) of these ratios with the total length of the leg and by the constants of differential growth (k) of the segments :

	Femur.	Tibia.	2nd tarsal segment.	Claw.	Total length of the leg.
Ratio : $\frac{\text{Length of the segment}}{\text{Length of the leg}}$.					
In relation to the total length of the leg : r .	0·555	0·215	—0·703	—0·376	
t .	2·31	0·557	3·43	1·44	
P .	0·02– 0·05	0·5– 0·7	<0·01	0·05– 0·1	
Values of k of the segments—					
In relation to the length of the body . . .	0·722	0·644	0·506	0·497	0·639
In relation to the length of the leg . . .	1·082	1·019	0·832	0·766	1·000

The relative length of the tibia shows no significant correlation with the length of the leg and the tibia appears to be almost isogonic with the total length ($k_{\text{tib}} \simeq k_{\text{leg}}$), the fact already indicated by the particularly high value of the correlation coefficient between absolute length of tibia and length of leg. The femur is positively heterogonic ($k_{\text{femur}} > k_{\text{leg}}$) and becomes relatively longer with the increasing length of the leg (r is positive, the significance being marginal). The 2nd tarsal segment and the claw are negatively heterogonic ($k_{\text{claw}} < k_{\text{2nd tars. segm.}} < k_{\text{leg}}$) and become relatively shorter ; the relative length of the tarsus shows significant negative correlation with the length of the leg, and for the claw the value of r is negative but non-significant. The centre of differential growth lies in the femur (fig. 5*b*) and the gradient decreases proximally with a steep fall between the tibia and tarsus. The above results show that the increase in the length of the leg is chiefly due to the lengthening of the proximal segments, while the distal segments contribute gradually less. It is perhaps interesting to mention that the values of k here obtained show great similarity to those calculated by Huxley (1932 : 85) from the results of Benazzi (1929) on regeneration of the limbs of the larva of the dragonfly *Aeschna grandis* during two instars. The corresponding values of k given by Huxley are : femur 1·12, tibia 1·02, tarsus 0·72.

The length of the tibia and tarsus, expressed as a fraction of the length of femur and tibia respectively have often been used as specific characters. Ferris (1918) found by experience that the relative lengths of these segments are variable among the individuals of the same species, and therefore the ratios are not constant. In so far as concerns *M. pini*, the different degrees of heterogony of each segment of the leg support his general conclusion, but indicate that the degree of variability of different ratios should be different. This is confirmed by the actual behaviour of the ratios tibia length/femur length and 2nd tars. segm. length/tibia length, which have been calculated and related to the total length of the leg. The former ratio varies from 1·048 to 0·943 (about 10 per cent.) and shows no significant correlation with the length of the leg ($P = 0{\cdot}5$–$0{\cdot}7$), although the value of r ($= - 0{\cdot}188$) is negative and perhaps in larger samples this ratio would show some degree of significant negative correlation. The ratio 2nd tars. segm. length/tibia length varies from 0·450 to 0·375 (about 20 per cent.) and shows significant negative correlation with the total length of the leg ($r = - 0{\cdot}688$; $P = < 0{\cdot}01$). It appears therefore that the use of the ratio tarsus length/tibia length is less reliable than that of the ratio tibia length/femur length.

The study of the relations between the lengths of particular segments of the antennae and the legs has revealed that in both organs each segment shows a different degree of differential growth in relation to the total length of the organ concerned. Consequently the ratios of the lengths of the particular segments to the length of the organ concerned, or the ratios between the segments of the same organ, are variable to a greater or lesser degree. Therefore the use of such ratios for separation of the closely related species, which are expected to show only small differences, seems to be unreliable, especially in cases such as *M. pini*, where the length of the legs and antennae varies considerably, leaving ample opportunity for conspicuous manifestation of the different degrees of heterogony of the component segments. In species in which these ratios differ to a degree which cannot be cancelled out by the differences in heterogony of the segments, the ratios may still be used for specific differentiation. It appears, for instance, that the difference of well over 20 per cent. in the values of the ratio tarsus length/tibia length could probably be used for separation of *M. pini* from the other species of the genus.

B. *Morphological Relationships of* M. pini *Green with the Other Species of the Genus.*

No specimens of species other than *M. pini* being available for study, the following comparison is based on published information only. Sixteen species of the genus are taken into consideration ; *M. sinensis* Chen (1937) is not discussed because no detailed information necessary for characterisation of this species has been available. Modern knowledge of the genus is based on the contribution by H. Morrison, who, in 1939, described ten new species and recognised the importance of certain minute characters for separation of the species ; the same line has been followed by McKenzie (1941). The descriptions of the other species, especially those described earlier (Kuwana, 1907 ; Herbert, 1919, 1921), contain few details now considered essential. Consequently the available data for characterisation of various species are by no means uniform. The adult female is best known ; the immature stages are much less known—in some species they were described from the cast skins only, or not at all. As a result, the relationship of the adult female given below is probably generally true, although detailed information on a few species is still badly needed. The suggested relationships of the immature stages are purely provisional. The study of a series of immature individuals of *M. pini* has revealed that, apart from a few characters (structural details of the spiracles) already recognised as important, certain other characters are remarkably constant ; some of these characters are casually mentioned in the descriptions, or are quite apparent from the published illustrations of a few species and appear to be different in different species. For instance, the 1st stage larvae of the species seem to differ in the distribution of the setae on the antennae and on the legs, in the relative length of the antennae, the legs, the tibia and tarsus, and the apical seta ; the characters involving relative lengths appear to show differences much greater than the probable correlation of these characters with the size of the body could produce. The number of pores in the spiracular pore plates seems to be of major importance in separation of the species at the intermediate stage. These characters may be of some, at least supplementary, importance for separation of the species, and are here suggested and tentatively employed.

The available information seems to indicate that the size of the stages, especially of the adult female of a particular species, varies considerably, and therefore the dimensions may be of importance only with regard to species differing markedly in size. The shape of the 1st stage larvae and of the adult females is fairly uniform throughout the genus. The intermediate stage of various species apparently differs in shape, but it is subjected to considerable distortion under the conditions in which it usually lives, and therefore the importance of the shape is limited to a few species with a characteristically formed posterior end to the abdomen.

1*st Stage larva*.—The 1st stage larva is the least known. The following characters appear to be of taxonomic importance: Structural details of the spiracles ; distribution of setae on the antennae and on the legs ; relative length of the antennae, of the anterior, middle, and posterior legs, and of the apical seta ; the relative length of the tarsus and tibia ; method of moulting, and the number of moults at this stage.

On the basis of similarity in the structure of the spiracles the 1st stage larva of *M. pini* falls in a group with, at present, *M. monophyllae* McKenzie, *M. vexillorum* Morrison, *M. alabamae* Morrison and *M. eduli* Morrison. The abdominal spiracles of these species open at the bottom of sclerotised cup-like depressions. As far as is known, *M. eduli* differs from *M. pini* and the other species of this group in having the cup-like depressions relatively large, the interspaces between

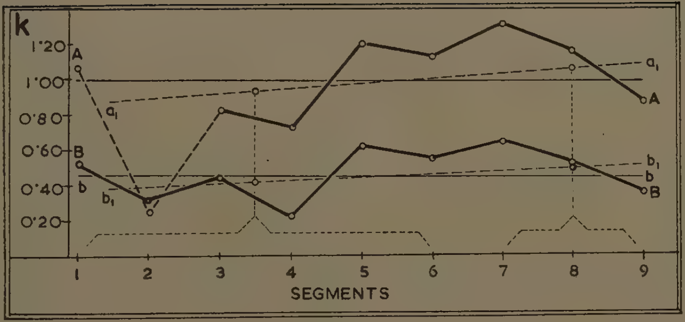

FIG. 5*a*.

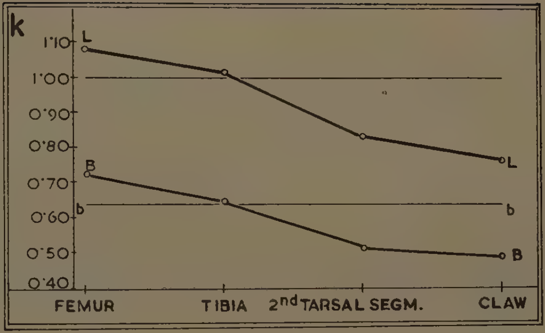

FIG. 5*b*.

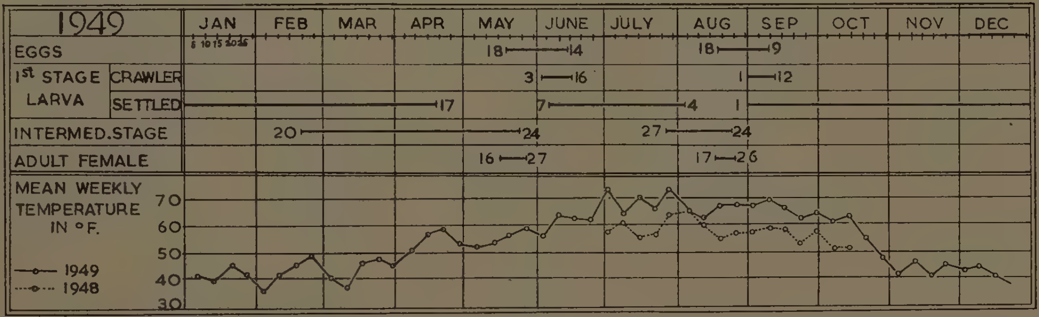

FIG. 6.

FIG. 5*a*.—Growth gradient and the values of k for particular segments of the antenna. A–A, in relation to the total length of the antenna; B–B, in relation to the length of the body; a_1–a_1, and b_1–b_1, the same for the length of the first six segments and of the last three segments. FIG. 5*b*.—Growth gradient, and values of k for femur, tibia, 2nd tarsal segment, and claw of the middle leg. L–L, in relation to the total length of the leg; B–B, in relation to the body length. FIG. 6.—Seasonal life cycle of *Matsucoccus pini* (Green), and the mean weekly temperatures as observed and recorded at I.C.S.T. Field Station at Silwood Park in 1949.

the invaginations being smaller than the diameter of the cup; in *M. pini* the interspaces between the invaginations are about twice the diameter of the cup. *M. pini* and *M. vexillorum* can be separated from each other by the relatively longer antenna in *M. pini*, and by the number of moults at this stage (two in *M. vexillorum*); the illustrations of this stage of *M. vexillorum* (McKenzie, 1943*a*) would suggest that the two species differ also in the distribution of the setae on the antennae, and in minute structural details of the spiracles. There is not sufficient published information to make possible the separation of *M. pini* from *M. alabamae* and *M. monophyllae*. Morrison's (1928) characterisation of the 1st stage larva of the genus probably refers to this stage of *M. alabamae*; this would indicate that *M. alabamae* differs from *M. pini* in having the tarsus considerably shorter than the tibia (both segments being subequal in *M. pini*), and in having the " anterior legs slightly larger," while in *M. pini* the anterior legs are noticeably shorter. *M. monophyllae* appears to have the apical seta relatively shorter than *M. pini* (cf. illustration of the 1st stage larva of *M. monophyllae* in McKenzie, 1941). In all three species differences in minute structural details of the spiracles, such as the diameter and depth of the cup-like depressions, distance between the depressions, etc., are also possible.

Intermediate stage.—The structural details of the spiracles provide the following set of important characters: absence or presence, and form of the spiracular depressions; number of pores in the spiracular pore plates; position of the opening of the trachea; presence or absence of a sub-atrium; relative size of the thoracic and abdominal spiracles. Some species have an apical notch with an internal vertical septum at the posterior end of the abdomen.

The intermediate stage of *M. pini* having no internal vertical septum at the posterior apex of the body, and having all spiracular depressions slanting at acute angles to the surface of the body, falls in a group with, at present, *M. fasciculensis* Herbert and *M. secretus* Morrison, the next closest being probably *M. vexillorum* Morrison and *M. monophyllae* McKenzie (the two latter species have been described from cast skins only). There is insufficient information to separate *M. pini* from *M. fasciculensis* at this stage. The position of the entrance of the trachea at the median side near the bottom of the spiracular depression in the thoracic spiracles appears to be a peculiar feature exhibited, as far as known, only by *M. pini*, and therefore separating it from all the other species. In addition, *M. pini* differs from the three species mentioned above by the following characters; having the abdominal spiracles conspicuously smaller than the thoracic spiracles it differs from *M. secretus*, where all spiracles are subequal; from *M. vexillorum* it differs in having the end of the abdomen with no " conical cauda-like extension," and a slightly smaller number of pores in the spiracular pore plates. Having 19–23 pores in the pore plate of the thoracic spiracles, and 16 decreasing to 7 pores in the posterior abdominal spiracles, it differs distinctly from *M. monophyllae*, which has 9 pores in the thoracic and 6 pores in the abdominal spiracles.

The adult female.—Statistical analysis of the characters of the adult female of *M. pini* has shown that both the number and the structural details of the derm pores are comparatively constant, and that the size of the dorsal cicatrices varies within a well defined range. Study of the published information on the other species revealed that these characters may also be used successfully for separation of the females of all the species of the genus.

On the basis of the presence or absence of the multilocular derm pores, the 16 species here discussed can be separated into two groups : (1) five species, the females of which have no multilocular derm pores, and (2) eleven species, the females of which have a cluster of multilocular derm pores at the posterior apex of the body. The second group can be further divided on the basis of the total number of the multilocular derm pores in the cluster, namely, (*a*) six species with 50–60 up to 100 multilocular derm pores in the cluster, and (*b*) five species with less than 50 multilocular derm pores in the cluster, the actual numbers being 13 to 44 pores. The female of *M. pini* with a total number of 30–37 pores belongs to the latter section, together with *M. monophyllae* McKenzie, *M. gallicolus* Morrison, *M. paucicicatrices* Morrison and, possibly, *M. matsumurae* Kuwana. *M. monophyllae* differs from *M. pini* (and the other species of the group) in having considerably larger dorsal cicatrices (diameter 15·2–28·5μ in *M. monophyllae*, and 4·2–9·5μ in *M. pini*) ; *M. gallicolus* is distinct in having smaller dorsal cicatrices (diameter 2·7–5·0μ) ; *M. paucicicatrices* differs from *M. pini* in having two sensory spines on the 5th to 9th segments of the antenna (never two such spines on the 5th segment in *M. pini*), and much fewer dorsal cicatrices (15–30 in *M. paucicicatrices*, 202–334 in *M. pini*). Apart from these characters, each of the five species differs by a different combination of the other characters, such as the actual number of multilocular derm pores, the number of bilocular derm pores in the first two abdominal rows, the length of the largest midventral seta, etc. (cf. IV : " Tentative Key for Identification of Adult females ").

C. *Morphological Relationship between* M. pini (*Green*) *and the type species*, M. matsumurae (*Kuwana*).

It is necessary to discuss separately the relationship between *M. pini* and the type species, *M. matsumurae*, because of the alleged identity of the two species (Morrison, 1928 : 53), although, from the remarks made by Ducasse (1941 : 217), it would appear that this view has since been abandoned. The difficulty in separating the two species lies in the fact that a modern description of the type species does not exist. In his original paper on *M. matsumurae* Kuwana (1907) described the adult female, the adult male, the 1st stage larva, and the egg. The intermediate stage was discovered by Kuwana much later and " turned over " to Herbert, who, on the occasion of his revision of the genus (1923), described it for the first time and also redescribed the other stages of this species. In the general description of the genus given by Morrison (1928) the description of the first stage larva is based " chiefly on genotype." However, both Herbert and Morrison based their conception of the type species on the specimens " from Japan and the eastern United States," of which the latter have later been recognised by Morrison (1939) as representing a distinct species, *M. alabamae* Morrison. There being no precise details of the material from which the actual descriptions of the particular stages were made, the information given by Herbert and Morrison leaves it uncertain as to whether they refer exclusively to one species, and, if so, to which. Moreover, all descriptions (including also a short account by F. Silvestri, 1939) contain very few of the details necessary for accurate identification of the species. A close study of the descriptions of various stages of *M. matsumurae* by Kuwana, Herbert and Morrison, and comparison of these with the description of *M. alabamae*, shows that the only description of the 1st stage larva which definitely refers to *M. matsumurae* is that given by Kuwana (1907). The intermediate stage, described by Herbert (1921), no doubt refers to the true *M. matsumurae* ; it differs obviously from that of *M. alabamae* (Morrison, 1939), which is known from cast skins only, while Herbert's description was made from complete specimens, evidently those received from Kuwana. All three descriptions of the adult female lack information necessary for modern specific diagnosis except the number of loculi in the multilocular derm pores, given by Morrison (1928). This detail refers either to *M. matsumurae* or to *M. alabamae*, but unfortunately is not mentioned in the subsequent (1939) description of the latter species. It appears that Japanese specimens of the adult female were available to Herbert and Morrison for study, and these might well have been primarily used in making the description. This assumption is here tentatively adopted, and the detail given by Morrison (1928) considered as referring to *M. matsumurae.*

The above information, though fragmentary, nevertheless provides enough data for definite conclusions. The 1st stage larvae of the two species differ, as far as known, in the following characters :

	M. matsumurae (Kuwana, 1907).	*M. pini.*
Body :		
Length . . .	189μ	345–456μ
Width	117μ	147–210μ
Antennae :		
Length . . .	91μ (apparently about ½ body length)	105–122μ less than ⅓ body length.
Tarsus :		
Length in relation to the tibia length	Shorter (apparently about ½ tibia length)	Subequal ; ratio 0·75–1·00 ; average 0·87.
Length of the apical seta .	(Apparently ¼ body length)	About ½ body length.

The intermediate stage of *M. matsumurae*, as described by Herbert (1921), differs from *M. pini* in having only the last 3–4 abdominal spiracular depressions slanting at an acute angle to the surface of the body ; in *M. pini* all spiracles show this condition conspicuously. It appears that the two species may differ also in the number of pores in the spiracular pore plates. According to Herbert, in *M. matsumurae* the pores occur in "large numbers," and his reproduction of the spiracle of this species shows 34 pores in the pore plate ; in *M. pini* the highest number of pores encountered in the largest 1st thoracic spiracles is 28 (range 19–28).

The adult female.—The only character which at present can be tentatively used for separation of the females of the two species is the number of loculi in the multilocular derm pores. In *M. pini* it varies from 10–12, the average being 10·6 ; according to Morrison (1928) there are up to 16 loculi in the type species, and in Herbert's illustration (1921, pl. III, fig. J) of the multilocular derm pore of *M. matsumurae* 14 loculi are drawn. This character is very constant in *M. pini* and is known to be constant in some other groups of Margarodidae, where small differences in the number of loculi in the derm pores are successfully used for separation of the species (Jakubski, 1950 ; and unpublished).

The morphological differences mentioned above seem to provide sufficient evidence for the conclusion that the two species are not identical. Further evidence to the same effect is apparent from the definitely different bionomics and geographical distributions of the two species. *M. pini* is parthenogenetic and bivoltine, confined to *Pinus sylvestris* and occurs in Southern England ; *M. matsumurae* is bisexual and univoltine, lives on *Pinus thunbergi* and occurs in Japan.

III. BIONOMICS.

A. *Habitat and Host Relations.*

Matsucoccus pini is apparently host specific and confined to Scots Pine, *Pinus sylvestris.* The insects are associated with partly separated bark scales covering still fresh and soft plant tissues on which the growing stages feed. These conditions are amply provided by the lower branches of the old pine trees and by both the main trunk and thicker branches of the younger trees, particularly those which grow in unfavourable conditions. On two occasions young trees which died in overcrowded and shaded positions showed signs of a preceding very heavy infestation. The heavy bark of the main trunk of old trees is not infested, nor are the higher branches of the vigorously growing crown. Thus, if there is an infestation, the lower peeling and unhealthy-looking branches will certainly harbour the insects, usually in quantity. Single trees, as well as those growing in groups or woods, are equally affected. There is no gall formation or necrotic change in the plant tissues attacked ; the only effect which can be assumed is that the growing insects, increasing considerably in size within the initially small enclosure under the bark scale, exert some pressure gradually lifting the partly separated scale and possibly causing rapid premature peeling.

Pines in Great Britain are heavily infested with *Pineus pini* (Adelginae), and the two insects may, and very often do occur together, sometimes the individuals of both being closely associated. *Pineus*, being more conspicuous, attracts more attention than the larval stages of *Matsucoccus*, which are concolorous with the surrounding plant tissues. This probably accounts for their being overlooked until recently.

B. *Life Cycle and Habits.*

Studies on the life cycle and habits of *Matsucoccus pini* were carried out at Silwood Park during the season 1948/49, and were based chiefly on field observations made two or three times a week. It was found impossible to follow individual development. The location of the larval stage of the insect necessitates the removal of the bark scale under which it is hidden. The 1st stage larva and the early intermediate forms seldom survive this operation undamaged, but even those apparently not injured sooner or later die (from desiccation ?) in spite of careful refixing of the bark scale or replacing it by a celluloid plate or tube around the twig. Therefore the approximate duration of each generation, as well as the duration of the particular stages, were computed from the recorded periods of occurrence. The field observations on incubation and on active life of both the first stage larva and the adult female were supplemented by breeding experiments and observations in the laboratory.

During the whole season no stages whatsoever of the male series were found in the field. To confirm the suspected monosexuality a series of breeding experiments were carried out. Altogether five females of the spring generation and 12 of the summer generation were obtained in the laboratory from fully grown intermediate forms collected some time (7–19 days) before the adults actually emerged. The intermediate forms have no genital opening and so any possibility of pre-adult fertilisation is excluded. Most of the females were kept singly in separate jars, and precautions taken to ensure that no other specimen of any kind of insect was present on the twigs. The behaviour of the virgin females thus obtained was identical with that of the females collected and observed in the field ; the numbers of eggs deposited were well within the normal ranges and the time of incubation and the mortality among the eggs were normal. The resulting larvae showed no difference in vigour, behaviour, or any other character, as compared with those of the larvae found active under natural conditions or obtained from the eggs collected in the field. It seems therefore quite safe to assume that the species is parthenogenetic.

So far, this is the first known instance of any species of the genus being parthenogenetic. The geographically nearest species, *M. feytaudi* from South-Western France (Les Landes), described and studied by Ducasse (1941), and the other eight better known species are bisexual. Unfortunately there is no information on this point with regard to the remaining seven species. It appears from the records that *M. pini* has a more northerly distribution than any other known species. The monosexuality of the British species may represent a case of " geographical parthenogenesis " in the sense of Vandel's conception (1928 : Suomalainen, 1950).

1. Seasonal life cycle.

Matsucoccus pini has two well separated generations in the year. The summer generation develops from eggs deposited in May and the adult females appear in the early autumn. The spring generation develops from eggs deposited in autumn, hibernates in the larval stages, and the adult females appear during the following May.

The seasonal life cycle (fig. 6), based on observations at Silwood Park in 1949, is as follows : The adult females of the spring generation which hibernated in the larval stages emerge gradually during the second half of May. Almost immediately after emergence each female proceeds with oviposition, which lasts from three to four days. The eggs hatch 17–21 days after deposition and the young larvae (crawlers) are to be found during the first half of June. Their active life is very short, and the first settled individuals of this stage are to be found almost simultaneously with the appearance of the first crawlers. The settled and rapidly growing larvae are present under the bark scales from the beginning of June till the first week in August. During this period the individual larvae exhibit increasing differences in the degree of their development. This is originally due to the gradual and prolonged period of hatching, and later apparently increased by local environmental conditions. At the end of July some of the already fully grown larvae begin to moult into the intermediate stage, the process being completed by all surviving individuals early in August. Thus the intermediate stage is found from the end of July till the end of August, when the adult females of the summer generation begin to appear. Adult females gradually emerge during the second half of August and at once proceed with oviposition. The eggs now deposited hatch in 9 to 19 days and the crawlers appear gradually during the first half of September. After settling under the bark scales growth is continued slowly during winter and they reach the full grown larval state in the spring. The differences in individual growth during this period are even greater than that of the corresponding stage in the summer. The earliest moult into the intermediate stage was observed on 20th February and the latest on 17th April ; thus the intermediate forms of this generation are to be found from the end of February onwards. The rates of development of the individual intermediate forms, however, seem to vary in such a way that all surviving individuals become fully grown about the middle of May ; during the second half of this month the adult females gradually emerge. The dates of the first appearance of the particular stages are as follows :

	Summer generation.				Spring generation.			
	Earliest observation (date).	Duration (days).	Fraction of the total period of development. Incubation.		Earliest observation (date).	Duration (days).	Fraction of the total period of development. Incubation.	
			Incl.	Excl.			Incl.	Excl.
Egg	18.v	.	.	.	18.viii	.	.	.
Incubation	.	16	0·17	—	.	14	0·055	—
1st larva	3.vi	.	.	.	1.ix	.	.	.
Duration	.	54	0·60	0·70	.	173	0·635	0·67
Intermediate	27.vii	.	.	.	20.ii	.	.	.
Duration	.	22	0·23	0·30	.	85	0·310	0·33
Adult female	17.viii	.	.	.	16.5	.	.	.
Total	18.v–17.viii	92	1·00	1·00	18.viii–16.v	272	1·00	1·00

It appears that the time required for complete development of the deposited eggs into adult females is 92 days in the summer and 272 days in the spring (hibernating) generation. Except for the incubation period, the actual number of days spent at a particular stage in the two generations differ considerably, but the relative durations as expressed in fractions of the total time required for the complete development are similar. The incubation period represents very unequal fractions, and if it is omitted the corresponding values of the relative duration of the other two stages are still closer—about 2/3 being taken by the 1st stage larva and about 1/3 by the intermediate stage.

It should be pointed out that the year 1949 was exceptionally warm, especially in the second half ; the mean weekly temperatures as recorded at Silwood Park during the year 1949 and part of 1948 are shown at the bottom of fig. 6. The mean weekly temperature from July to October, 1949, was from 3·8° F. to 15·6° F (average 8·9° F.) higher than in the corresponding period in 1948. Apparently because of this factor the females of the summer generation in 1949 appeared as early as the second half of August, while in 1948 they were observed in the middle of September. The labels of the specimens available to Green bear October, 1923, as the date of their collection. The time of appearance of the females of the spring (hibernating) generation seems to be constant ; the known specimens of females of this generation, including those of Green (1924) and those found at Silwood Park in 1948, 1949 and 1950 were all collected in May.

2. Habits.

a. *Adult female.*—Shortly before emergence the completely formed adult female can be seen compressed and enclosed tightly within the transparent skin of the previous stage. Observations on exposed individuals in the laboratory 2 to 3 days before emerging showed that the female exhibits distinct movements of a peristaltic nature ; the constrictions begin somewhere on the middle of the body, and run posteriorly in waves lasting 1 to 2 seconds at irregular intervals of 15 to 65 seconds. The intervals in one of the recorded series were : . . . 20, 65, 15, 25, 25, 15, 25, 25, 20, 20, 40, 20, 25 . . . seconds. There is no apparent change in the frequency towards the time of ecdysis. When finally the old skin breaks, splitting characteristically into five flaps at the posterior end of the body, the peristaltic movements continue in short series alternating with longer periods of complete rest. Gradually bulging through the opening, the female backs its way out and in the final stage of liberation helps itself by apparently haphazard movements of the legs. Under laboratory conditions (exposed individuals) the time required for liberation after the break of the skin varies from 45 minutes to over six hours ; in natural conditions the pressure of the surrounding plant tissues may provide some help and speed up both the break of the skin and the subsequent liberation of the female. Often, however, the female fails to complete the ecdysis and is found dead half-way out of the previous skin. After ecdysis the female remains quiet for 1 to 2 hours, the only sign of life being the trembling antennae and sporadic contractions of the legs. Gradually co-ordinated movements appear and the female begins to walk, dragging the swollen abdomen and feeling its way by continuously moving the antennae. In both generations the period of emergence is prolonged and the individual females appear gradually over a period of 2 to 3 weeks ; the same has been observed in the laboratory. On 8th August, 1949, some branches of pine with fully grown intermediate individuals were brought in and kept under observation in the laboratory. The first female emerged on 15th August and was followed by two on 16th, one on 17th, five on 19th, two on 20th, six between 21st and 26th, and the last surviving female emerged on 30th August. At the time of their appearance in the field the females are to be found singly wandering about on the bark of the main trunk of young trees, and on the thicker branches of the lower part of both young and old trees. Occasionally they may be encountered on the main trunk of old trees covered with heavy bark and then they seem generally to move upwards. Elsewhere there is no definite direction to their migration—up or down, towards the main trunk or away from it, along or around the branches. They always walk in zig-zags and circles, making a very irregular track and continually investigating the cracks and crevices in the bark. Placed on a sheet of paper the female travels along a similar track with frequent turnings and crossings of the path previously made, and in 30 minutes is capable of covering about 45 to 70 cm., though the actual distance from the starting-point is always much less, about 10 to 25 cm.

It appears that the duration of active life of the female depends on the availability of suitable shelters for oviposition. The shortest period of activity observed in young females which emerged in the laboratory and which were provided with a suitable branch of pine, was about 4 hours, but it varies individually, and in apparently identical conditions a female may be active for any period up to 24 hours. Immediately after the female has placed itself in a suitable sheltered position the secretion of the ovisac begins and in the next 12 hours the first eggs are laid. Females which were kept at the bottom of an empty Petri dish, though very weak, were still active after five or six days ; at that time they showed only scanty waxy covering on the abdomen and had laid no eggs. In natural conditions, with plenty of shelters at hand, the female is probably active for several hours only. This, together with the prolonged period during which the females gradually emerge, would account for the comparatively small number of active females observed at any one time on a tree known to be heavily infested. During the assumed short active life in natural conditions the female may cover a distance of from several inches to a few yards. It is capable, however, of prolonging the activity for several days, and migrates much farther in case of emergency (e.g., falling on the ground).

The site for oviposition may be any crack or crevice in the bark or under the bark scales of the host tree. The favourite sites are the axils of the branches, where wrinkled rings of the bark provide many suitable shelters, and from there the ovipositing females may be obtained comparatively easily. Females may, however, also be found under the bark scales on the branches at any distance from the axils, or under the separated bark of a dead and dry terminal twig, or even in empty tunnels made by boring larvae of other insects. Two individuals which apparently fell off the tree were found with ovisacs formed and ovipositing in the axils of *Erica tetralix* growing under the infested pine. After suitable shelter has been found the female wedges its head and thorax deep into the narrowest part of the crevice, stretches its legs and, with falcate claws inserted in the plant tissues, fixes herself firmly in this position. The swollen abdomen filled with eggs remains projecting into the more spacious part of the crack. In about 12 hours after settling a loosely woven ovisac is formed and oviposition begins. The ovisac is composed of fine waxy threads secreted from the glands of the abdomen ; in the anterior part of the body only a few waxy threads appear on margins of the thorax and on the head. The secretion of the ovisac continues till a later stage in the process of oviposition. The ovisac, even when fully formed, is of a very delicate texture, and when exposed breaks easily under the weight of the contained eggs. This would suggest that for the proper protection of the eggs a well-sheltered position for the ovipositing female and for the ovisac is essential. The number of eggs laid by a female varies from 56 to 98 (average 75) in the spring generation, and from 30 to 92 (average 61) in the summer generation. It appears that the larger females lay more eggs, but this was not proved decisively because of the difficulties in making satisfactory mounts of females of which the ovisacs had been examined. Oviposition lasts from 3 to 4 days. About two-thirds of the total number of eggs are deposited during the first 24 hours, the bulk of the remainder during the second day, while on the third (and fourth) day only a few remaining eggs are laid. A few eggs often remain inside the body of the female. Females examined at various times during the process of oviposition show feverish trembling of the antennae and slow peristaltic pulsation of the abdomen, which ceases about the 3rd day of oviposition ; at that time the female is dead, shrivelled, especially the abdomen, which now forms a small appendix to the thorax. The genital opening of the dead female remains wide open after completed oviposition.

As already mentioned, females which were kept in the laboratory and were provided with suitable branches on which to settle did so within 4 to 24 hours ; in the next 2 to 4 days each of the 20 females kept in this way deposited a number of eggs varying from 40 to 92. Seven females were kept at the bottom of an empty Petri dish and these, after 5 to 6 days of continuous activity, placed themselves in the angle between the bottom and the sides of the dish and began to spin ovisacs. On the 5th day one of them was transferred under a bark scale and, before it died, deposited 30 eggs in the next two days. The remaining six females were kept in the dish till the end, and two laid 5 and 14 eggs respectively, while the other four did not oviposit at all. It appears that for normal oviposition the enclosure of the female within a small space is essential, thus suggesting that the insects show thigmokinesis at oviposition.

b. *Incubation.*—The eggs deposited hatch in 11 to 21 days in May (1949) and in 10 to 18 days in September (1949). The eggs kept under ordinary laboratory conditions hatched 2 to 3 days earlier. The differences in the time of incubation may be due to the temperature ; the mean weekly temperature in May, 1949, was 52–57° F. and in September 68·6–62·4° F., and the indoor temperature is usually higher than that in the open. In the last third of the incubation period the red eye-spots of the developing embryo are visible through the egg-shell.

The development of the embryo in the egg is independent of deposition. The eggs laid last contain partly developed embryos, and preparations of females mounted after oviposition was completed showed that the eggs which are not deposited also develop normally. These eggs may hatch in due course, and the larvae perhaps escape through the wide-open genital opening of the dead female. Further evidence on this point is provided by the observation made on females which were kept in Petri dishes and laid a few eggs or none at all. These females were mounted 14 to 18 days after their apparent death and each showed the abdomen full of eggs containing embryos at various stages of development, including fully formed larvae. One of the females which did not oviposit at all was accidentally damaged before mounting, and among the eggs inside the body there were a few young living larvae which had hatched out inside the female and were exhibiting feeble movements of legs and antennae similar to the post-natal movements of normally hatched larvae.

c. *The* 1*st stage larva.—Hatching :* The larvae from an individual ovisac hatch out gradually over a period of 2 to 3 days. The newly born larvae, often with the egg shell attached to the apical setae or to the legs, remain quiet among the waxy threads of the ovisac, exhibiting only sporadic feeble movements of the antennae and the legs. This post-natal rest lasts from about one to several hours, after which the larvae crawl out, pushing their way through the loosely felted ovisac, and begin their migration.

Active life.—At this time the larvae are very inconspicuous and small, with red eye-spots, and the amber-yellow colour of the body matches the similar yellow-reddish colour of the young bark. In its activities the 1st stage larva generally resembles the adult female. While walking the antennae are stretched forwards, feeling the way in front of the insect; the two apical setae are dragged behind, being kept continuously in touch with the surface crawled upon. The track made by the larva is very irregular, with frequent turnings and circles; the cracks and spaces under the bark scales are being investigated all the time.

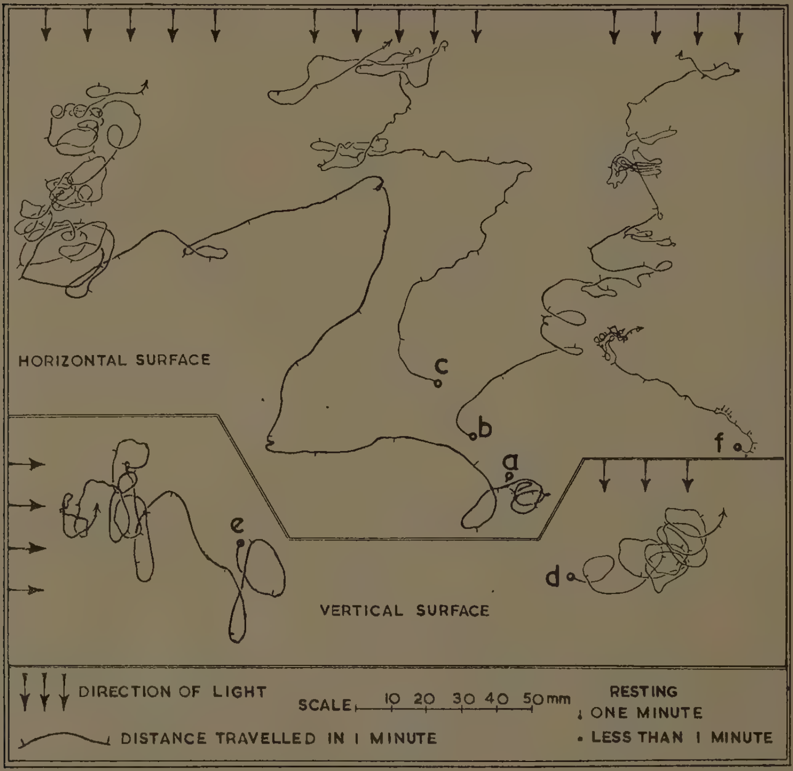
HORIZONTAL SURFACE
VERTICAL SURFACE
a
b
c
d
e
f
DIRECTION OF LIGHT
SCALE 10 20 30 40 50 mm
RESTING
ONE MINUTE
LESS THAN 1 MINUTE
DISTANCE TRAVELLED IN 1 MINUTE

Fig. 7.—Tracks made by the 1st stage larvae; *a*, *b*, *c* on horizontal surface with the dispersed light falling obliquely from the top and above; *d*, *e*, on vertical surface with the dispersed light falling from above and from left side respectively; *f*, track made by a larva after 3 days of continuous activity in empty glass tube (conditions as for *a*, *b*, *c*).

Although there is no apparently definite direction of the migration, the larvae seem to move gradually away from the main trunk. Placed on a sheet of rough paper in the laboratory the larvae travel along similar tracks, five of which are reproduced in fig. 7. Each track was made by a different larva of more or less the same age, i.e., larvae hatched during the night and tested the following morning when in full vigour. Three (*a*, *b*, *c*) represent the tracks made by the larvae placed on a horizontal surface with dispersed light falling obliquely from the top and above ; the other two (*d*, *e*) the tracks made by the larvae placed on a vertical surface with dispersed light falling from above (*d*) and from the left side (*e*) respectively. The tracks made suggest that the larvae are negatively geotactic and respond positively to light. The distance travelled per unit of time by each larva tested is remarkably constant (22–26 mm. per minute). There is no difference in speed at different light intensities, i.e., there appears to be no orthokinesis but, as the rate of turning increases at higher light intensities, it is suggested that the larvae show klinokinesis. It is perhaps interesting to note that once a larva has begun to turn clockwise (*b*), or anticlockwise (*a*, *c*, *d*, *e*), it continues to do so all the time.

It appears that in the field the active life of the 1st stage larva is short, and that the duration of activity depends on the availability of suitable feeding sites. Newly hatched larvae which were provided in the laboratory with a suitable fresh branch of pine on which to settle did so within two to several hours. Larvae which were kept in an empty glass tube remained active for 3 to 4 days ; on the third day they became considerably less active, walked sluggishly at variable speeds with frequent stops and hesitations (fig. 7, *f*) and on the fourth day all were dead.

Settling.—Normally the larvae settle under partly separated bark scales ; occasionally they may be found in cracks and crevices. They push themselves deeply towards the far end of the space under the bark scale or crevice where the plant tissues are still fresh and soft, insert their mouthparts and begin to feed. They are unable to settle on exposed fresh tissues after the bark scale has been removed. In a few hours after settling the larvae secrete a narrow fringe of white waxy secretion along the margins of the abdomen and become incapable of movement ; larvae which settled within four hours of being released showed only feeble movements of their antennae and legs when disturbed. Once the larvae settle they cannot be induced to withdraw their mouthparts from the plant tissues, and when removed mechanically, even those apparently not injured are incapable of resuming their migration and reinserting their proboscis. At settling the larvae do not show any tendency to aggregate and are usually found widely separated from each other, sometimes in loose groups of 2 to 5 individuals, occasionally in widely spaced rows.

During the following growing period the larvae remain stationary, increase considerably in size and assume a more or less pyriform shape when fully grown (cf. " Description of the Stages." p. 287). In about the last quarter of the growing period the larger mouthparts of the intermediate instar are being formed far in front of the larval ones and can be seen on mounted specimens. At ecdysis the skin breaks anteriorly (see p. 292), and at this time the new mouthparts are already inserted in the plant tissues.

d. *The Intermediate stage*.—The intermediate (apodous) stage remains stationary with the larval skin encircling the posterior half of the body. Small tufts of fine waxy threads appear from the spiracular depressions. The insect continues to feed at this stage and the size of the body increases considerably, the fully grown intermediate form being almost twice the linear dimensions of young individual immediately after shedding the larval skin. The determination of the time at which feeding ceases is difficult. A number of fully grown individuals with completely formed females visible through the transparent skin were removed from the branches and were kept in a glass dish ; these invariably failed to moult into adult females. The individuals of a similar sample which were not removed from the twigs began to moult in four to seven days. The females dissected out from the intermediate stage reveal the mouthparts still attached to their bodies. It would appear therefore that feeding (or imbibing of water ?) perhaps continues until or very nearly until the moment of ecdysis.

c. *Mortality during the Development.*

The mortality among the deposited eggs is very low. In the field, as well as in the laboratory, about 5 per cent. dry and shrivelled eggs remain in the ovisac after the newly hatched larvae have deserted it. The growing period of the 1st stage larvae seems to be most critical for the species. At the time of settlement the young larvae are to be found in numbers under practically every bark scale on an infested branch ; at the time of their full growth there are comparatively few living individuals left. Counts of the dead bodies of the individuals apparently belonging to the particular generation studied would indicate that in both summer and hibernating generations about 60 to 80 per cent. of young larvae die at various stages of growth. During the growing period of the intermediate stage the mortality is also considerable. Similar counts as for the 1st stage larva reveal that about 21 per cent. of the young individuals of this stage reach a fully grown state from which the adult females emerge. Thus in the whole cycle the cumulative mortality appears to be about 92 to 96 per cent. and only 8 to 4 per cent. of the eggs deposited develop into adult females. The above estimation does not include possible losses of complete ovisacs and adult females for which birds may be responsible.

The causes of death are obscure. There are no traces of internal parasites. The Cecidomyiid larva usually associated with *Pineus pini* (Barnes, 1927, 1930 ; Wilson, 1939) was once observed attacking and killing the intermediate form in the laboratory when three of these larvae were kept in a glass jar with several intermediate individuals of *M. pini*, but the attack was not performed eagerly, probably because these larvae " do not feed whilst exposed " (Wilson, 1939, p. 380). The mites, *Hemisarcoptes malus* Shimer (= *H. coccisugus* Lignieres) and *Cheyletia flabellifera* Michael (det. T. E. Hughes), both of which are predacious, are associated with *M. pini* and may kill immature stages. Finally Chrysopid larvae are to be found on the bark of the branches infested by *Matsucoccus pini* and *Pineus pini* and may be responsible for killing some of them. It seems possible that, at least in some cases, death results from mechanical and environmental conditions, i.e., pressure of the surrounding plant tissues, lack of food in drying branches, desiccation, etc.

d. *Geographical Distribution.*

The original specimens of adult females of *M. pini* available to E. E. Green for study were collected from *Pinus sylvestris* from Surrey, Oxshott, in October, 1923, and in May, 1924. On my visit there on 26th February, 1949, I found a great abundance of 1st stage larvae developed to various degrees. Apart from the above, specimens of *M. pini* were obtained from the following localities :

Berks : Silwood Park, Sunninghill, where, during the season 1948/49, the present study was carried out. On single trees and on trees growing in ornamental groups ; very abundant.

Surrey : Pyrford, near Woking, 31.i.1949. Two larvae in an advanced stage of growth on a branch of Scots pine sent to me by Mr. and Mrs. M. Tupper.

Wimbledon Common. On several occasions during the year 1949 ; various stages. On single trees and on trees growing in groups ; abundant.

Richmond Park, 26.iii.1949. 1st stage larvae and individuals in the process of moulting into intermediate stage. On trees growing in groups ; abundant.

Lower Barnes, Farnham, 3.iii.1949. 1st stage larva and an intermediate form just after moulting. On a twig from a young pine tree growing in a garden, sent to me by Miss E. Debenham.

Bagshot. On several occasions during 1949 ; all stages. Pine forest ; very abundant.

E. Sussex : Highwood, and Ashburn Park, near Bexhill-on-Sea, 17.iv.1949. Advanced 1st stage larvae and early intermediate forms. On trees growing in groups and in forests ; abundant.

Hants : Hordle, New Milton, 4.ix.1949. Fully grown intermediate forms and cast skins. On trees growing in groups by the side of the road ; abundant. A thorough search for adult females was not possible in the circumstances of my visit there.

No specimens of *M. pini* were found on a few pines (*Pinus sylvestris*) encountered on Guernsey (C.I.) in the summer of 1949, and no positive results were obtained while searching pine trees in the vicinity of Cardiff (South Wales) in 1950.

There is no positive or negative information on distribution from any localities other than those mentioned above. So far as is known, *M. pini* is limited in its distribution to Southern England.

IV. TENTATIVE KEY FOR IDENTIFICATION OF THE FEMALES OF THE SPECIES OF THE GENUS *MATSUCOCCUS* CKLL.

Note.—Owing to lack of sufficient information *Matsucoccus sinensis* Chen (1937) is not included in the key. For the same reasons the characterisation of various species in the key is by no means uniform, and the position of a few species, especially that of the genotype *M. matsumurae*, provisional.

1. All derm pores of bilocular type, including those at posterior apex of body. On abdominal segments the derm pores normally not arranged in transverse rows, and those at posterior end of abdomen scattered or forming an apical cluster. Antennae and legs reduced or normal. Dorsal cicatrices confined to dorsum or extending to margins and reaching the venter . . . . 2.

– Derm pores at posterior apex of multilocular type, there forming a distinct apical cluster. On abdomen the bilocular pores arranged in transverse rows. Antennae and legs normal. Dorsal cicatrices confined to dorsum of abdomen . . . . 6.

2. Antennae less than 9 segmented. Legs more or less reduced. Dorsal cicatrices extending to margins and reaching the venter. No cluster of derm pores at posterior apex of body, and no derm pores on anterior part of body . . . . 3.

– Antennae 9 segmented. Legs normal. Dorsal cicatrices confined to dorsum of abdomen . . . . 4.

3. Antennae 6 or 7 segmented; last three segments with stout sensory setae. Legs more or less reduced. Bilocular derm pores, a few scattered, at posterior end of the body only. Dorsal cicatrices small, 7–10·5μ in diameter, in four transverse rows, the last extending to ventral side, and with an additional cluster of about 50 cicatrices at the posterior apex; total number of cicatrices about 216. Body setae few, small. Spiracles obscure. On *Pinus occidentalis* (*cubensis*); Dominican Republic . . . . . **subdegeneratus** Morrison

– Antennae reduced to 2–3 segments, with one sensory seta at apex. Legs reduced. Bilocular derm pores on last three segments of abdomen only. Dorsal cicatrices 6·5–11μ in diameter; in 5–6 rows on dorsum and on margins, reaching far over the ventral side of abdomen; total number about 243. Body setae few, scattered; midventral abdominal setae large, about 27μ long. Spiracles, 2 thoracic and 7 abdominal; the thoracic larger. On *Pinus ponderosa*, *Pinus* sp.; Arizona, Mexico . . . . **degeneratus** Morrison

4. Segments 6 to 9 of antenna each with two sensory spines. On *Pinus monophylla*; Idaho, U.S.A . . . . **acalyptus** Herbert

– Segments 5 to 9 of antenna each with two sensory spines . . . . 5.

5. Dorsal cicatrices large, 15–23μ in diameter; numerous, 450 or more (up to 770); in transverse rows, the number of rows being variable (up to 10). Bilocular derm pores on margins and at posterior apex of body. Largest midventral abdominal seta about 75μ long. On *Pinus ponderosa*; Western U.S.A. . . . . **secretus** Morrison

– Dorsal cicatrices large on dorsum; in transverse rows; total number 300 or less. Bilocular derm pores scattered on dorsum and venter, and in a cluster at posterior apex of body. Midventral abdominal setae about 50μ long. Derm rough and crinkled. On *Pinus sabiniana*, *P. ponderosa*; California, U.S.A. . . **fasciculensis** Herbert

6. Apical cluster composed of less than 50 multilocular derm pores (13–44) 7.

– Apical cluster composed of more than 50 multilocular derm pores (50–60, up to 100) . . . . 11.

7. Total number of dorsal cicatrices 15–30; these small, 4·7–6·8μ in diameter, scattered on middorsal part of posterior abdominal segments. Segments 5 to 9 of antennae with two sensory spines. Multilocular derm pores at posterior apex of abdomen in a cluster of 20–40 pores. Bilocular derm pores in anterior part of body confined to margins; on abdomen in rows, the 1st abdominal row (reduced) composed of 15–20 pores. On *Pinus lambertiana*, *P. monticola*, *P. flexilis*; California, Oregon, Montana, Wyoming (U.S.A.) **paucicicatrices** Morrison

– Total number of dorsal cicatrices 150–350. Segments 6 to 9 of antennae each with two sensory spines . . . . 8.

8. Dorsal cicatrices large, 15·2–28·5μ in diameter; in 6 rows totalling 165–284 (average 213). In the apical cluster 28–44 multilocular derm pores. Each of the first two abdominal rows composed of 43–84 bilocular derm pores. Largest midventral seta 22·8μ long. On *Pinus monophylla*; California (U.S.A.) . . . **monophyllae** McKenzie

– Dorsal cicatrices small, less than 15μ in diameter . . . . 9.

9. Dorsal cicatrices very small, 2·7–5μ in diameter (average 3·5μ); in 5 to 10 rows on intermediate abdominal segments; total number 150–350 (average 241). Apical cluster composed of 13–31 multilocular derm pores. Largest midventral seta about 42μ long. On *Pinus rigida*, *P. echinata*, *P. ponderosa*; Eastern U.S.A. **gallicolus** Morrison

– Dorsal cicatrices 4·2–12μ in diameter . . . . 10.

10. Dorsal cicatrices about 9μ in diameter. Multilocular derm pores with 14–16 peripheral loculi. On *Pinus thunbergi*; Japan **matsumurae** (Kuwana)

– Dorsal cicatrices 4·2–9·5μ in diameter; in 5 bands on dorsum of 3rd to 7th abdominal segments, the 1st and 5th bands more or less reduced; total number 202–334 (average 282). Apical cluster composed of 30–37 multilocular derm pores; these with 10–12 peripheral loculi. The 1st (incomplete) abdominal row with 21–28 bilocular pores; the 2nd abdominal row with 25–35 pores. Largest midventral seta 28–38μ long. Fifth segment of antennae occasionally with one small sensory spine. Trochanter normally with one seta (60–70μ long), occasionally a second, smaller (21–42μ long) seta is present on one or two, rarely three or four legs of an insect. Derm apparently double, composed of two partly separated cuticles. On *Pinus sylvestris*; Southern England . . . . **pini** (Green)

11. Trochanter with two setae, each 68–90μ long. Dorsal cicatrices 5–7μ in diameter, in 5–7 transverse bands; total number 180–280. Multilocular derm pores in an apical cluster composed of 60–90 pores. Each of first two abdominal rows composed of 30–50 bilocular derm pores. Largest midventral seta 30–41μ long. Segments 6 to 9 of antenna each with a pair of stout sensory spines; the 5th segment with one similar, but smaller sensory spine. On *Pinus contorta*, *P. scopulorum*, *P. ponderosa*, *P. jeffreyi*, *P. sabiniana*; California, Oregon, Arizona (U.S.A.) . . . . **bisetosus** Morrison

– Trochanter normally with one seta. Number of multilocular derm pores, number of dorsal cicatrices, number of bilocular derm pores in first two abdominal rows, and length of midventral seta never in combination as in *M. bisetosus* . . . . 12.

12. Apical cluster composed of about 100 multilocular derm pores. Dorsal cicatrices totalling 150. Bilocular derm pores on ventral side of body larger (about 11·5μ in diameter), those on dorsal side smaller (about 7·6μ diameter). On *Pinus maritima*; South-West France (Les Landes) . . . . **feytaudi** Ducasse

– Apical cluster with 50 to 80 multilocular derm pores . . . . 13.

13. Dorsal cicatrices comparatively small, 3·6–9μ in diameter; in 5–8 bands, totalling 400–800, usually 600–700. Apical cluster composed of 70–80 multilocular derm pores. Each of first two abdominal rows composed of 50–60 bilocular derm pores. Largest midventral seta 18μ long, or less. On *Pinus ponderosa* var. *scopulorum*; Arizona, New Mexico (U.S.A.) . . . . **vexillorum** Morrison

– Dorsal cicatrices 7–14μ in diameter, totalling 150–300. Apical cluster composed of 50–75 multilocular derm pores. In each of first two abdominal rows 25 (or less), or about 30 bilocular derm pores . . 14.

14. Bilocular derm pores in anterior part of body generally scattered, but forming a band of about 30 ducts between third coxae and 2nd thoracic spiracles; each of first two abdominal rows composed of 30 bilocular derm pores. Dorsal cicatrices 7–7·5μ in diameter; in 6

transverse rows, totalling about 260. Largest midventral seta about 45μ long. Apical cluster composed of 50–75 multilocular derm pores. On *Pinus eduli* ; Arizona (U.S.A.) . . . . **eduli** Morrison

– No transverse band of bilocular derm pores between 3rd pair of coxae and 2nd thoracic spiracles. Dorsal cicatrices 7·5–14μ in diameter ; in 3–5 rows, totalling 150–300. Largest midventral seta 16μ long or less . . . . 15.

15. In each of first two abdominal rows 25 or less bilocular derm pores ; central duct of bilocular derm pores uniformly widened towards inner end. Dorsal cicatrices 7·5–9·5μ in diameter ; in 3–4 transverse rows, totalling about 150–200. Apical cluster composed of 50–60 multilocular derm pores. Largest midventral seta 15μ long (usually 12–13μ). On *Pinus ponderosa* : California (U.S.A.) **californicus** Morrison

– In each of first two abdominal rows 30 bilocular derm pores ; their central duct plainly swollen and lobate at inner end. Dorsal cicatrices 8–14μ in diameter (variable) ; in 4 to 5 transverse clusters, totalling 200–300. Apical cluster composed of 50–70 multilocular derm pores. Largest midventral seta about 16μ long. On *Pinus* spp. ; Alabama (U.S.A.) . . . . **alabamae** Morrison

V. SUMMARY.

1. The morphology and bionomics of *Matsucoccus pini* (Green) have been studied.

2. The adult female is redescribed, and the other stages, which include the egg, the 1st stage larva, and the intermediate stage, are described for the first time.

3. The species is parthenogenetic and has two well-separated generations in the year. The summer generation develops in 3 months, from June to August-September ; the spring generation develops in 9 months, from September to the following May, hibernating in the immature stage (1st stage larva.)

4. A statistical analysis shows that :

(*a*) The females of the two generations differ significantly in the size of the body, those of the summer generation being smaller.

(*b*) The structural details of the derm pores, the number of multilocular and bilocular derm pores, and the size of the dorsal cicatrices are independent of the size of the insect.

(*c*) The length of the antennae, the length of the legs, the total number of dorsal cicatrices and the length of the largest mid-ventral seta are positively correlated with the length of the body, all being negatively heterogonic with it.

(*d*) Each segment of the antennae and legs shows a different degree of heterogony in relation to the total length of the corresponding organ. In the antennae the centre of heterogonic growth lies in the 7th segment, decreasing both proximally and distally ; in the leg this centre lies in the femur and decreases distally. Consequently the characters involving the relative length of the segments such as " antennal formula " or expressing the length of a segment as a fraction of another are variable.

5. The morphological relationships of the stages of *M. pini* with the corresponding stages of the other species are discussed. The suggested relationships of the immature stages are provisional. The adult female of *M. pini* falls in a group with *M. monophyllae* Morrison, *M. gallicolus* Morrison, *M. paucicicatrices* Morrison and probably *M. matsumurae* (Kuwana); all these species are characterised by having the multilocular derm pores in a posterior apical cluster composed of less than 50 pores. A tentative key for identification of the females of the species is appended.

6. Comparison of the stages of *M. pini* with *M. matsumurae*, based on the existing information on the latter, shows that the two species are not identical.

7. *M. pini* is confined to *Pinus sylvestris*, young and old trees, single and growing in groups or woods, being equally affected. There is no gall formation or necrotic change in the host tissues.

8. The habits of the stages are described. The adult female and the 1st stage larva are the only active stages, the duration of the active life of both being short (several hours). Enclosure within a small space of both the female at oviposition and the larva at settling is essential, thus suggesting that they show thigmokinesis. In their behaviour the larvae exhibit negative geotaxis, positive response to light, and they seem to show klinokinesis, but not orthokinesis.

9. In both generations the cumulative mortality during development is about 92–96 per cent. The causes of death are obscure; Cecidomyid and Chrysopid larvae, mites, desiccation and mechanical pressure of the bark may be responsible. There are no internal parasites.

10. So far as is known, *M. pini* is limited in its geographical distribution to Southern England.

VI. References.

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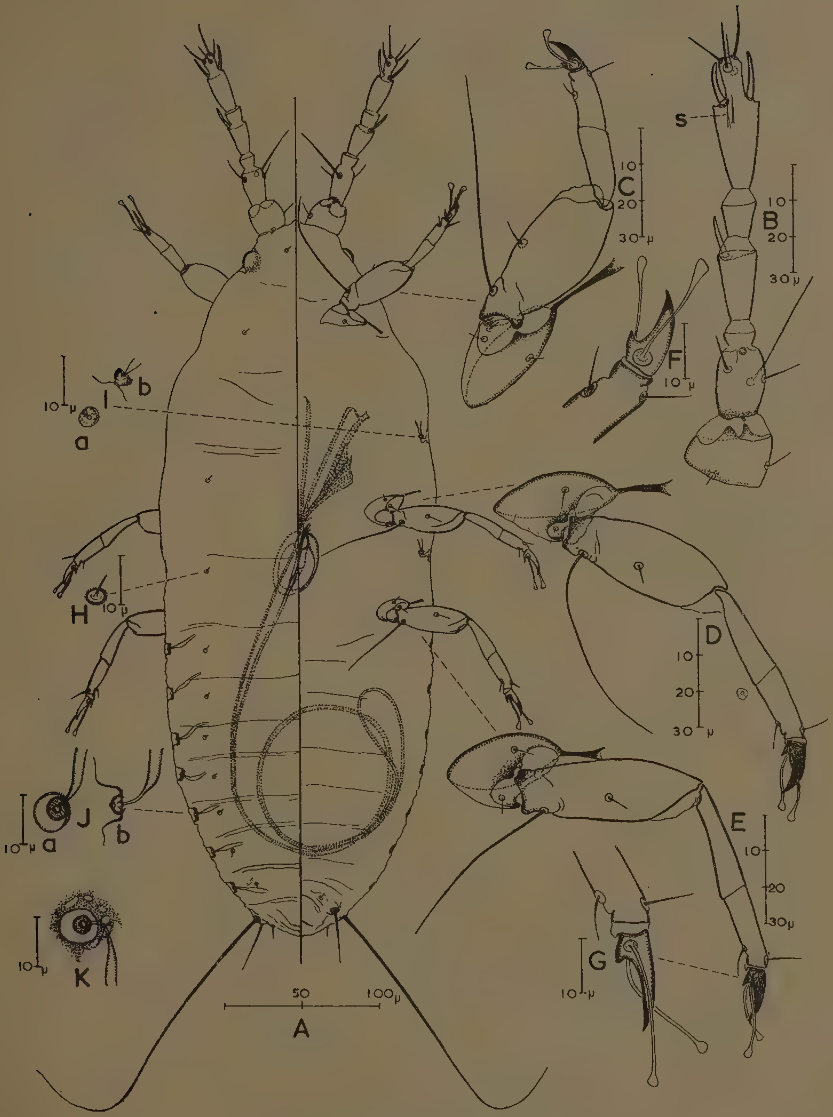
PLATE I.—1ST STAGE LARVA.

A, general outline, dorsal and ventral.
B, antenna ; S, sclerotised struts.
C, anterior, D, middle, E, posterior legs.
F, and G, detail of the claw of the anterior and posterior legs.
H, derm seta from the subdorsal row.
I, thoracic spiracle, surface view (*a*) and section (*b*).
J, abdominal spiracle, surface view (*a*) and section (*b*).
K, surface view of the abdominal spiracle of a fully grown larva showing sclerotised derm around the spiracular depression.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Matsucoccus pini (Green). 1st Stage Larva.

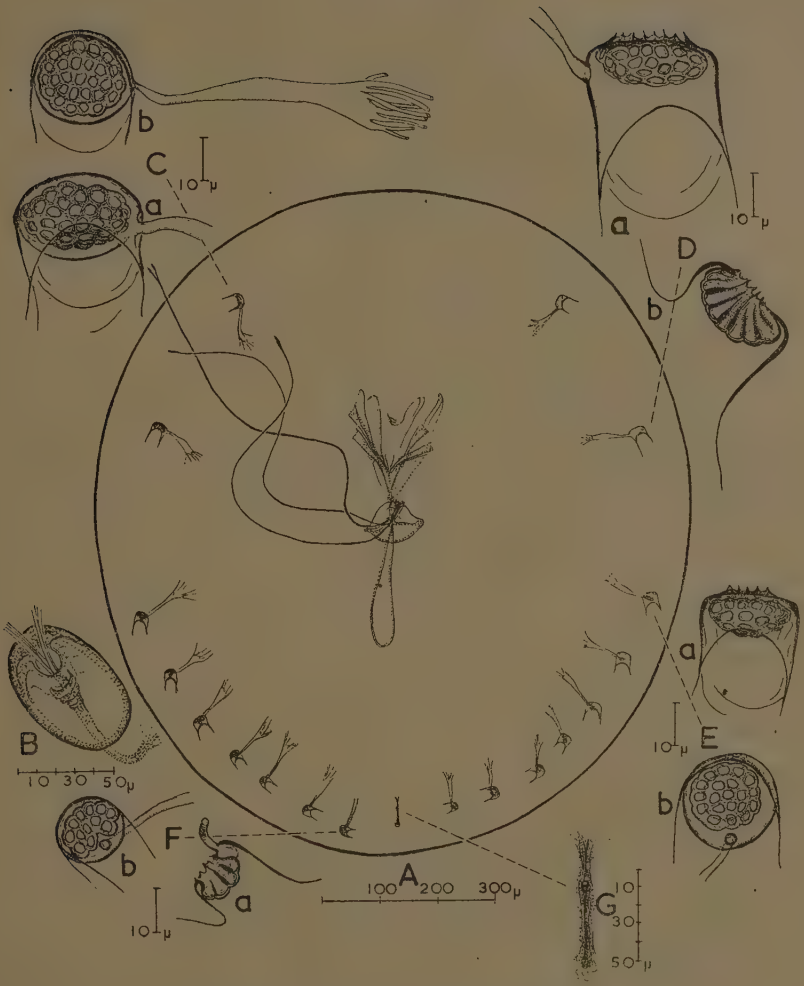
PLATE II.—INTERMEDIATE STAGE.

A, general outline, ventral.

B, labium, anterior view.

C–F, spiracles ; C, Ist thoracic, surface view (*a*) and pore plate (*b*) ; D, IInd thoracic, surface view (*a*) and section (*b*) ; E, 1st abdominal, surface view (*a*) and pore plate (*b*) ; F, 7th abdominal, section (*a*) and pore plate (*b*).

G, median subventral suture at the posterior apex of the body.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Matsucoccus pini (Green). Intermediate stage.

Plate III.—Adult Female.

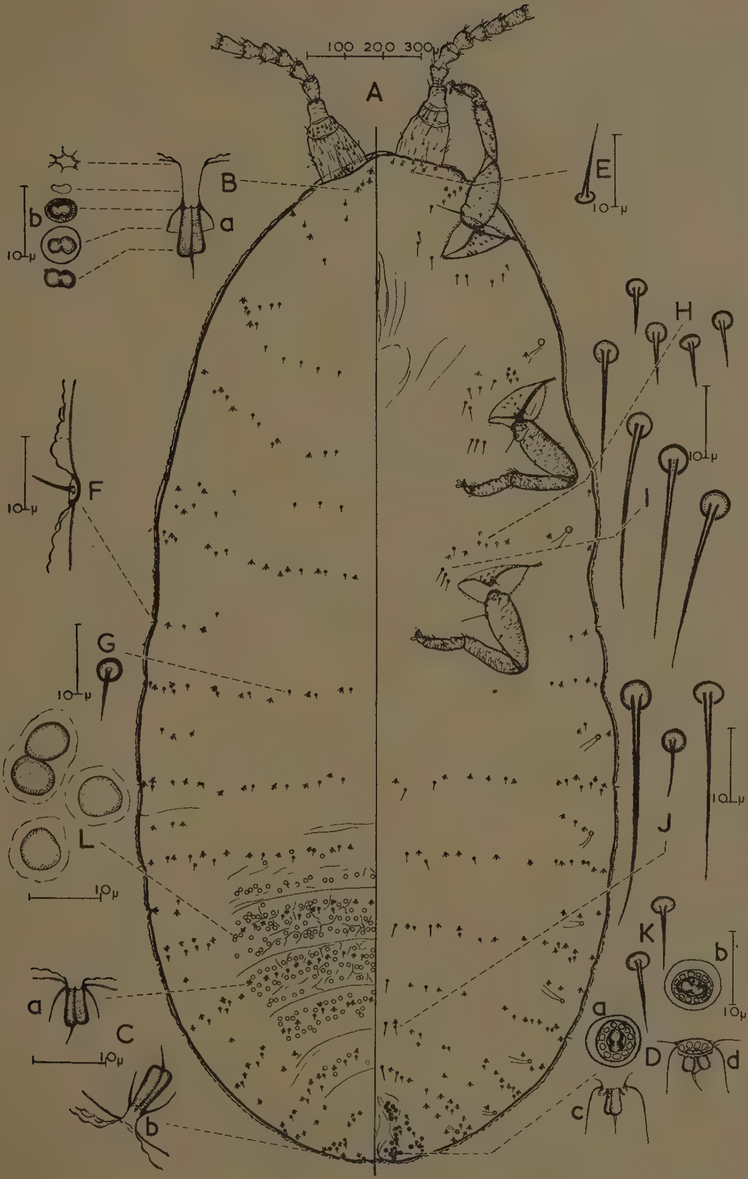
A, general outline, dorsal and ventral.

B, C, bilocular derm pores: B, from the head, longitudinal section (*a*) and transverse sections at various levels (*b*); C, from abdomen, sections.

D, multilocular derm pores, surface view (*a*, *b*) and section (*c*, *d*).

E–K, derm setae: E, from the head; F, from the margin; G, from the dorsum; H, precoxal group; I, intercoxal group; J, midventral; K, from the posterior apex.

L, Dorsal cicatrices.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Matsucoccus pini (Green). Adult Female.

PLATE IV.—ADULT FEMALE (*cont.*).

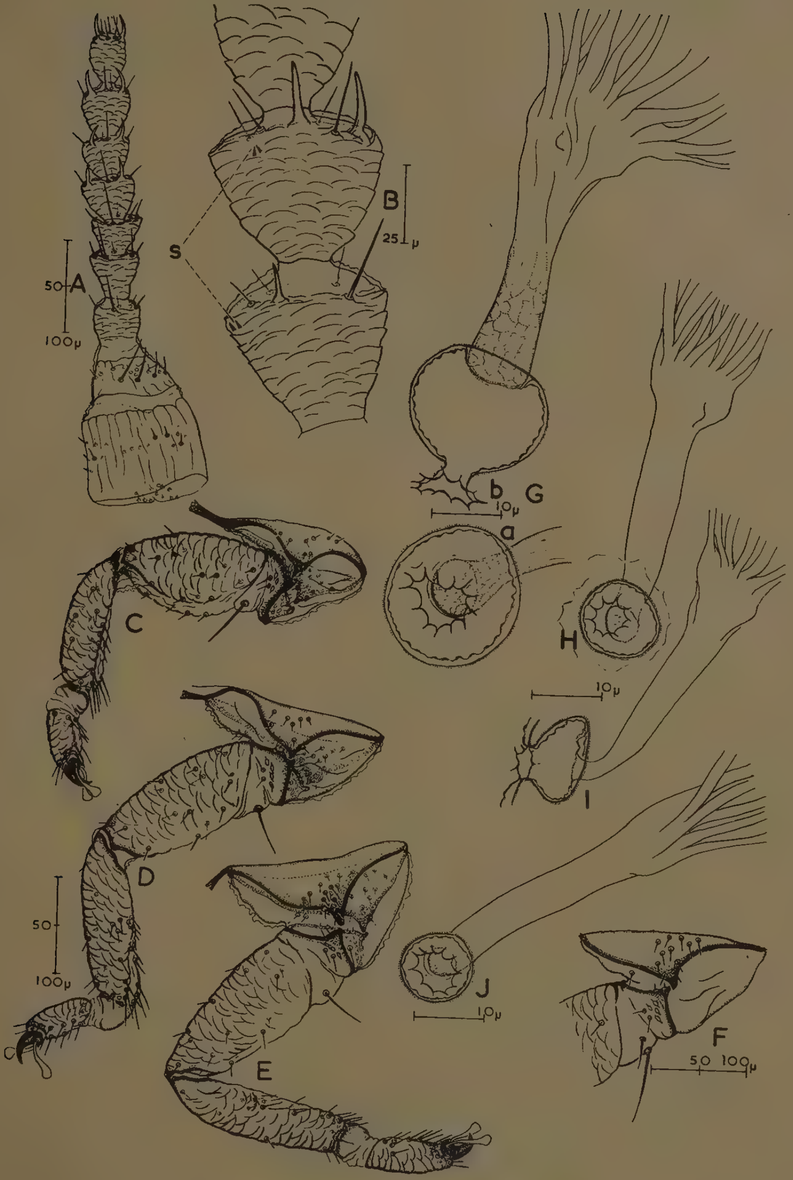
A, left antenna in ventral aspect.

B, segments 5 and 6 of the left antenna, ventral aspect; showing occasional condition of the 5th segment with single small spine; *s*, sclerotised struts.

C, anterior, D, middle, E, posterior legs.

F, occasional condition of the trochanter with two setae.

G–J, Spiracles: G, prothoracic, surface view (*a*) and section (*b*). H, 1st abdominal, surface view: I, 4th abdominal, section; J, 7th abdominal, surface view.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Matsucoccus pini (Green). Adult Female.

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4 plates, 7 figs.

31st December, 1952

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THE GENERA OF THE CASSIDINAE (COLEOPTERA: CHRYSOMELIDAE).

By W. D. Hincks, M.Sc., F.R.E.S.

(*Manchester Museum.*)

Manuscript received 12th January, 1952.

(Read 1st October, 1952).

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1. Introduction.

During the years before the war the late Dr. Franz Spaeth was engaged in preparing a manuscript on the Cassidinae for publication in Wytsman's *Genera Insectorum*. With the outbreak of war the original plan of the work was modified to include the species as well as the genera, with the view of producing a monographic revision of the subfamily. It seems probable that this manuscript was completed sometime in 1942. Unfortunately, however, the first copy appears to have been totally destroyed when the printer's premises in Vienna were damaged by bombing. The writer (Hincks, 1950*b*, 1951) has already explained how a very incomplete second copy came to be confided to his care.

During the course of his work Dr. Spaeth reviewed all the genera previously established and was able to reduce a number of them to the status of subgenera or synonyms. In addition he erected some new genera and subgenera which became necessary as his revision proceeded. Before receiving the Spaeth manuscript the writer undertook to produce a new edition of Spaeth's Cassidinae catalogue (1914) and had already reviewed the nomenclature of some of the genera (Hincks, 1950*a*). Subsequent emendations to the International Code of Nomenclature in 1948 have caused several of the conclusions reached in this paper to require modification. Rather than publish these corrections alone it has been thought a useful plan to prepare a complete list of all the genonyms used in the Cassidinae, selecting types where these do not appear to have been designated previously, bringing the nomenclature into line with the Rules, and indicating the conclusions reached by Spaeth. In addition the new generic and subgeneric descriptions included in the manuscript have been added, in their original German, and these should be credited to Spaeth. A few comments by the writer are printed in English. In one or two instances Spaeth's genera had either invalid names or were not described in the manuscript available. These have been described by the present writer.

The systematic list here included foreshadows the sequence and status of the groups which is being followed in the forthcoming new catalogue of the subfamily. Types of the few new species described are in the Spaeth Collection now preserved in the Manchester Museum.

The writer wishes to record his cordial thanks to Dipl. Ing. Franz Spaeth, of Vienna, for placing the literary relics of Dr. Spaeth in his hands. To his colleague, Mr. Frank Willett, M.A., he is indebted for much assistance in the translation of the Key to Tribes and for supervising his transcription of Spaeth's descriptions.

2. KEY TO TRIBES (AFTER UNPUBLISHED MANUSCRIPT OF DR. F. SPAETH).

1 (10) Metasternal episternum fused with mesosternal epimeron.
2 (5) First and second abdominal sternites fused; at least anterior angles of pronotum with pore and tactile bristle; prosternum strongly expanded behind, its margin truncate.
3 (4) Both anterior and posterior angles of pronotum with pores and bristles; labrum with longitudinal median carina; anterior margin of prosternum with a shallow median emargination; mouthparts partly covered by prosternum and separated from base of antennae by an elongate, quadrate or rectangular clypeus, the sides of which do not converge above Tribe 7. **Spilophorini**
4 (3) Only anterior angles of pronotum with pore and bristle; labrum without median carina; anterior margin of prosternum without median emargination; clypeus very short, ridge-like or subtriangular in form, mouthparts therefore very close to base of antennae . . . . Tribe 6. **Imatidiini**
5 (2) First and second abdominal sternites not fused.
6 (9) Mouthparts free; clypeus not longer than broad.
7 (8) Anterior angles of pronotum with pore and bristle; prosternum broad between anterior coxae, not expanded behind; mesosternum deeply emarginate, the emargination deepened for the reception of the prosternal process and thickened behind and at the sides; antennae short and thick, the distal segments transverse . . . . Tribe 5. **Hemisphaerotini**
8 (7) Pores, bristles and true anterior angles of pronotum absent; the lateral areas of latter appearing as broad lobes, rounded in front; prosternum narrow between anterior coxae, its process strongly expanded with truncate margin; mesosternum truncate in front, not margined behind; antennae long and slender, the distal segments longer than broad . . Tribe 4. **Delocraniini**
9 (6) Mouthparts partly hidden by anterior margin of prosternum Tribe 1. **Notosacanthini**
10 (1) Metasternal episternum not entirely fused with mesosternal epimeron, only occasionally indistinctly connected.
11 (14) Antennae (except proximal segments) with progressively increasing longitudinal striations; segments cylindrical, not narrower at base than apex of preceding segment, closely approximated, without clear demarcation between proximal and distal seg-

ments ; head directed vertically, vertex and eyes higher than mouth, both visible from above ; claws untoothed.

12 (13) Mouthparts free ; clypeus very short, more than twice as broad as long, broadly rounded above with a blunt triangular median point, arcuately emarginate below ; distal segments of antennae from fourth or fifth with round cross-section Tribe 2. **Epistictinini**

13 (12) Mouthparts hidden by anterior margin of prosternum ; clypeus approximating to an equilateral triangle, longer and narrower than in the Epistictinini, its lower margin almost straight ; distal segments of antennae somewhat flattened, with elliptical cross section beginning not earlier than sixth segment Tribe 3. **Basiprionotini**

14 (11) Antennae without longitudinal sculpture on distal segments.

15 (16) Claws approximated, directed backwards, more or less parallel ; occasionally one claw missing . . . . . . Tribe 10. **Dorynotini**

16 (15) Claws diverging

17 (32) Head sloping, clypeus more or less directed upwards, eyes higher than mouthparts.

18 (19) Claw segment strongly expanded towards apex and obscuring base or whole of claws, which are therefore hidden from above ; claws with basal tooth ; elytra metallic, with confused punctuation, and without groove separating disc from lateral areas . . . . Tribe 11. **Eugenysini**

19 (18) Claw segment of normal breadth, claws visible from above.

20 (21) Distal antennal segments not commencing before sixth segment and differently formed from the proximal, being thickly covered with hair, much longer, of equal thickness throughout ; proximal segments, on the other hand, shining, shorter, hairless, each segment with slenderer base and broader apex ; prosternum broad, usually quite flat, a little expanded behind ; claws untoothed . . . . Tribe 8. **Omocerini**

21 (20) Distal antennal segments commencing before sixth segment and differing less in length and shape from proximal segments.

22 (25) Claw or claw segment with tooth-like process.

23 (24) Claws toothed, elytra with confused puncturation, without a groove differentiating disc from lateral margins ; inner margin of epipleurae reaching suture well before apex ; all species without opalescence . . . . Tribe 12. **Stolaini**

24 (23) Claws untoothed, although claw segment terminates in tooth-like process which is longitudinally depressed medially so as to project over the claw on each side like a tooth ; elytra with serial puncturation, disc separated from lateral areas by a discontinuous line of punctures ; inner margin of epipleurae reaching suture shortly before, and continuing with it to, the apex ; upper surface yellow, opalescent in life (**Enagria,** subgenus of **Physonota,** Tribe 15. **Physonotini**)

25 (22) Claws and claw segment untoothed.

26 (27) Anterior part of head or vertex exposed by being incompletely covered by pronotum, in dorsal view ; prosternum between anterior coxae taking the form of a narrow rounded keel, only exceptionally with a shallow impression ; upperside black or metallic, sometimes with yellow markings, but never opalescent Tribe 9. **Goniocheniini**

27 (26) Head entirely hidden by pronotum so that not even the anterior part is visible in dorsal view; anterior margin of pronotum never emarginate.

28 (29) Posterior angles of pronotum acute and produced behind so as to lie in close proximity to, and extending narrowly beneath, humeral angles of elytra; latter cuneiform, with completely or nearly uniformly convex upperside; puncturation serial; prosternum between anterior coxae narrow, forming a rounded keel without impression; posterior coxae not salient Tribe 13. **Ischyrosonychini**

29 (28) Posterior angles of pronotum not produced; outline ovate or rounded, never, as in the Eurypedini, cuneiform.

30 (31) Lateral areas of elytra very narrow, with thickened margins; prosternum broad between anterior coxae, convex, expanded behind into a broad, flat, lanceolate process; upperside without opalescence; antennae yellow, except for three reddish proximal segments . . . . Tribe 14. **Asterizini**

31 (30) Lateral areas of elytra broad, margins never thickened; distal segments of antennae at least partially black; upperside predominantly yellow, opalescent in life . . . Tribe 15. **Physonotini**

32 (17) Head horizontal, completely covered by pronotum and not visible from above; anterior margin of pronotum not emarginate (except *Hybosa cynthia* Boh., in which the pronotum is emarginate in front and the head partially visible).

33 (40) Claws of intermediate, posterior, or all legs at least with inner comb-teeth or striation.

34 (35) Old world species (Asia, Africa, Australia, and neighbouring islands); claws shell-shaped, the same on all legs, always combed, never with striation on inner side but sometimes on outer; third antennal segment always longer than second, and, with rare exceptions, also longer than fourth Tribe 16. **Aspidomorphini**

35 (34) Tropical American species; claws not shell-shaped, inner and outer sides equally combed or striated; in some Charidotini with a basal tooth on claws of anterior legs.

36 (37) Third antennal segment shorter than second; claws striated on all legs, or with comb teeth on all legs or only on intermediate and posterior legs when the anterior legs have a basal tooth on claws . . . . Tribe 19. **Charidotini**

37 (36) Third antennal segment longer than second.

38 (39) Claws of intermediate and posterior legs with comb teeth, those of anterior legs with a basal tooth . . . (**Ctenophilaspis** of Tribe 19)

39 (38) All claws with striation but without comb teeth (a few American Cassidini, namely subgenera *Dyscineta*, *Psalidonota* and *Podostraba* of *Coptocycla* and also genus *Metrionaspis*).

40 (33) Claws without comb-teeth or striation, smooth or toothed.

41 (42) Metasternal episternum inflated, projecting beyond outer margin of epimeron and connecting with an emargination in the elytral epipleurae; pronotum trapezoidal, widened in front, enclosed almost to anterior margin by the greatly produced humeral angles of elytra . . . . Tribe 17. **Basiptini**

42 (41) Metasternal episternum not inflated and not strikingly projecting beyond outer margin of epimeron into the epipleurae Tribe 18. **Cassidini**

3. SYSTEMATIC LIST OF TRIBES, GENERA, SUBGENERA AND THEIR TYPE SPECIES.

Tribe 1. **Notosacanthini** (*Hoplionotites* Chapuis *partim*, *Hoplionotitae* Spaeth).

1. *Notosacantha* Chevrolat *in* Dejean, 1837 : 367, 391, monobasic, *Cassida echinata* Fabricius, 1801.

Hoplionota Hope, 1840 : 152, 153 (*Hoplionata err. typ.*), *C. echinata* Fabricius, by original designation.

Thyreomorpha (Dejean, 1837 : 367, 391, *nom. nud.*) Boheman, 1850 : 35, monobasic, *Hoplionota badia* Boheman, 1850.

2. *Herminella* Spaeth, 1913*b* : 529, monobasic, *H. marshalli*, Spaeth, 1913.

Tribe 2. **Epistictinini** (*Priopterites* Chapuis *partim*, *Epistictitae* Spaeth).

1. *Androya* Spaeth, 1911 : 239, *Metriopepla rubrocostata* Fairmaire, 1898, by present designation.

2. *Metriopepla* Fairmaire, 1882*a* : 57, monobasic, (*M. lividula* Fairmaire, 1882 =) *M. inornata* Waterhouse, C. O., 1877.

3. *Epistictina* Hincks, 1950*a* : 509, new name for *Epistictia* Boheman, 1850 *nec* Amyot, 1847.

Epistictia Boheman, 1850 : 12, *E. viridimaculata* Boheman, 1850, by designation of Maulik, 1919 : 318.

Tribe 3. **Basiprionotini** (*Priopterites* Chapuis *partim*, *Priopteritae* Spaeth).

1. *Basiprionota* Chevrolat *in* Dejean, 1837 : 367, 391, monobasic, *Cassida octopunctata* Fabricius, 1787.

Prioptera Hope, 1840 : 152, 153, 176, *C. octopunctata* Fabricius, by original designation.

a. *Stenoprioptera* Spaeth, 1914*b* : 132, monobasic, *S. tibetana* Spaeth, 1914. (Subgenus).

2. *Megapyga* Boheman, 1850 : 3, 40, *M. eximia* Boheman, 1850, by present designation.

3. *Craspedonta* Chevrolat *in* Dejean, 1837 : 367, 391, monobasic, *Cassida leyana* (= *leayana*) Latreille, 1807.

Calopepla Hope, 1840 : 152, *C. leyana* (= *leayana*) Latreille, 1807, by original designation.

4. **Pseudandroya** Spaeth, gen. n. (p. 343), monobasic, *Calopepla livingstonei* Baly, 1864.

5. *Cassidopsis* Fairmaire, 1899 : 557, monobasic, *C. basipennis* Fairmaire, 1899.

Tribe 4. **Delocraniini** (*Hoplionotites* Chapuis *partim*, *Delocraniitae* Spaeth).

1. *Delocrania* Guérin-Méneville, 1844 : pl. 141, monobasic, *D. cossyphoides* Guérin-Méneville, 1844.

Tribe 5. **Hemisphaerotini** (*Himatidiites* Chapuis *partim*, *Porphyraspitae* Spaeth).

1. *Spaethiella* Barber and Bridwell, 1940 : 11, new name for *Hemisphaerota* Spaeth, 1905 *nec* Chevrolat, 1837.

Hemisphaerota Spaeth, 1905 : 82, *Imatidium sanguineum* Fabricius, 1801, by designation of Barber and Bridwell, 1940 : 11.

2. *Hemisphaerota* Chevrolat *in* Dejean, 1837 : 367, 391, *Cassida erythrocera* Germar, 1824, by designation of Duponchel and Chevrolat *in* D'Orbigny, 1843 : 210.

Porphyraspis Hope, 1840 : 152, 154, *C. erythrocera* Germar, 1824, by original designation.

Emperochela Spaeth, 1901*b* : 333, *partim*, *Porphyraspis palmarum* Boheman, 1856, by original designation.

Tribe 6. **Imatidiini** (*Himatidiites* Chapuis *partim*, *Himatidiititae* Spaeth).[1]

1. *Imatidium* Fabricius, 1801 : 345, *I. thoracicum* Fabricius, 1801, by designation of Latreille, 1810 : 432.
    Himatidium auctt.
    a. *Parimatidium* Spaeth, 1938 : 307, *I. rubrum* Boheman, 1850, by original designation. (Subgenus).
2. *Calliaspis* Dejean, 1837 : 367, 391, monobasic, *Cassida rubra* Olivier, 1808.
    Calliaspis Boheman, 1850 : 81.
    Cyanaspis Weise, 1904 : 433, monobasic, *C. testaceicornis* Weise, 1904.
3. *Stilpnaspis* Weise, 1905 : 298, monobasic, *S. marginata* Weise, 1905.
4. **Spaethaspis** Hincks, gen. n. (p. 343), monobasic, *S. lloydi* Hincks, sp. n. (p. 344).

Tribe 7. **Spilophorini** (*Spilophorites* Chapuis, *Spilophoritae* Spaeth).

1. *Spilophora* Boheman, 1850 : 107, *Imatidium trimaculatum* Fabricius, 1801, by present designation.
    Imatidium Hope, 1840 : 152 (*nec* Fabricius).
2. *Calyptocephala* Chevrolat *in* Dejean, 1837 : 367, 391, monobasic, *Cassida nigricornis* Germar, 1824.

Tribe 8. **Omocerini** (*Tauromites* Chapuis, *Tauromitae* Spaeth).

1. *Polychalca* Chevrolat *in* Dejean, 1837 : 368, 392, *Cassida* (*variolosa* Fabricius, 1801, *nec* Olivier, 1790 =) *punctatissima* Wolf, 1818, by designation of Duponchel and Chevrolat *in* D'Orbigny, 1843 : 211.
    Pilidionota Spaeth, 1913*c* : 128, *Cassida variolosa* Fabricius, 1801, by original designation.
    Muzonia Spaeth, 1913*c* : 130, monobasic, *Canistra nigroaenea* Boheman, 1856. **(syn. n.)**
    a. *Desmonata* Hope, 1839 : 97, *Cassida platynota* Germar, 1824, by original designation. (Subgenus).
2. *Omocerus* Chevrolat, 1835 : 119, *Cassida bicornis* Linnaeus, 1763, by designation of Duponchel and Chevrolat *in* D'Orbigny, 1843 : 211.
    Himatidium Illiger, 1804, *partim*.
    Tauroma Hope, 1839 : 97, *Cassida taurus* Fabricius, 1787, by original designation.
    a. *Paratauroma* Spaeth, 1913*c* : 127, *Tauroma casta* Boheman, 1862, by original designation. (Subgenus).
    b. *Platytauroma* Spaeth, 1913*c* : 127, *Tauroma coracina* Boheman, 1850, by present designation. (Subgenus).
    c. *Nebroma* Spaeth, 1913*c* : 126, *Cassida malachitica* Germar, 1824, by present designation. (Subgenus).
3. *Cyclosoma* Guérin-Méneville, 1835 : pl. 48, f. 5, monobasic, *Cassida* (*longicornis* Guérin-Méneville, 1835 =) *palliata* Fabricius, 1787.
    Prenea Spaeth, 1913*c* : 129, *Cassida palliata* Fabricius, 1787, by present designation.

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[1] The first three genera of this tribe are regarded as members of the Hispinae by Monrós and Viana (1951, *Acta zool. Lilloana* **11** : 369).

a. *Dolichotoma* Hope, 1839 : 95, *D. chloris* Hope, 1839, by original designation. (Subgenus).

b. *Proglima* Hincks, 1950*a* : 511, new name for *Glima* Spaeth, 1913, *nec Glymma* de Marseul, 1856. (Subgenus).

Glima Spaeth, 1913*c* : 129, *Dolichotoma mirabilis* Boheman, 1856, by designation of Hincks, 1950*a* : 511.

4. *Discomorpha* Chevrolat *in* Dejean, 1837 : 368, 392, *Cassida variegata* (Fabricius =) Linnaeus, 1758, by designation of Duponchel and Chevrolat *in* D'Orbigny, 1843 : 211.

Oxynodera Hope, 1840 : 160, 184, *Cassida variegata* Linnaeus, by original designation.

Bia Weise, 1896*b* : 31, *Cassida variegata* Linnaeus, by original designation.

a. *Vulpia* Spaeth, 1913*c* : 129, *Bia latissima* Spaeth, 1902, by original designation. (Subgenus).

b. *Paravulpia* Spaeth, 1940 : 143, monobasic, *Dolichotoma speciosa* Baly, 1859. (Subgenus).

5. *Canistra* Erichson, 1847 : 151, *C. varicosa* Erichson, 1847, by original designation.

Canistrella Spaeth, 1913*c* : 131, *Oxynodera rubiginosa* Guérin-Méneville, 1844, by original designation.

6. *Cassidinoma* Hincks, 1950*a* : 508, new name for *Oma* Spaeth, 1913, *nec Omma* Newman, 1839.

Oma Spaeth, 1913*c* : 128, *Desmonata denticulata* Boheman, 1850, by designation of Hincks, 1950*a* : 509.

7. *Carlobruchia* Spaeth, 1911 : 244, new name for *Bruchia* Spaeth, 1907, *nec* Weise, 1906.

Bruchia Spaeth, 1907 : 153, monobasic, *B. tricostata* Spaeth, 1907.

a. *Smodingonota* Spaeth, 1913*c* : 130, *Cassida carbonaria* Klug, 1829, by original designation. (Subgenus).

Tribe 9. **Goniocheniini** (*Goniocheniitae* Spaeth).

1. *Zeugonota* Spaeth, 1913*c* : 128, *Desmonata quadrinodosa* Boheman, 1856, by present designation.

2. **Chlamydocassis** Spaeth, gen. n. (p. 344), *Cassida metallica* Klug, 1829, by present designation.

3. *Polychalma* Barber and Bridwell, 1940 : 8, 9, new name for *Polychalca* Weise, 1900, *nec* Chevrolat, 1837.

Polychalca Weise, 1900*b* : 460, *Cassida multicava* Latreille, 1821, by designation of Weise, 1900*b* : 460 (*multivaca err.*!)

4. *Goniochenia* Weise, 1896*a* : 10, *Mesomphalia quadraticollis* Boheman, 1850, by designation of Spaeth, 1914*c* : 29.

a. *Baranosa* Weise, 1899*b* : 268, *B.* (*decolor* Weise, 1899 =) *haroldi* (Wagener, 1877) by present designation. (Subgenus).

5. *Herissa* Spaeth, 1909*a* : 724, monobasic, *Chelymorpha pantherina* Blanchard, 1837–43.

Tribe 10. **Dorynotini** (*Batonotites* Chapuis, *Batonotitae* Spaeth).

1. *Dorynota* Chevrolat *in* Dejean, 1837 : 370, 394, *Cassida bidens* Fabricius, 1781, by designation of Duponchel and Chevrolat *in* D'Orbigny, 1843 : 211.

Batonota Hope, 1839 : 98, *Cassida bidens* Fabricius, by original designation.

a. *Akantaka* Maulik, 1916 : 583, *Batonota viridisignata* Boheman, 1854, by Monrós and Viana, 1949 : 414. (Subgenus). (Given generic rank by Monrós and Viana, 1949).

2. *Paranota* Monrós and Viana, 1949 : 396, *Batonota ensifera* Boheman, 1854, by original designation.
3. *Paratrikona* Spaeth, 1923 : 66, *Batonota turrifera* Boheman, 1854, by designation of Monrós and Viana, 1949 : 413.
4. *Omoteina* Chevrolat *in* Dejean, 1837 : 374, 398, monobasic, *Cassida humeralis* Olivier, 1808.
   Trikona Maulik, 1916 : 583, *Cassida humeralis* Olivier, by present designation.
5. *Heteronychocassis* Spaeth, 1915*c* : 285, monobasic, *H. acuticollis* Spaeth, 1915.
6. *Eremionycha* Spaeth, 1911 : 259, monobasic, *E.* (*miraculosa* Spaeth, 1911 =) *bahiana* (Boheman, 1855).

Tribe 11. **Eugenysini** (*Mesomphaliites* Chapuis *partim*, *Calaspideitae* Spaeth).

1. *Eugenysa* Chevrolat *in* Dejean, 1837 : 368, 392, monobasic, *Cassida grossa* Linnaeus, 1758.
   Calaspidea Hope, 1840 : 183, *Cassida grossa* Linnaeus, by original designation.
   Calaspis Hope, 1840 : 160 (*errore*).
2. *Miocalaspis* Weise, 1899*b* : 270, monobasic, *M.* (*conspersa* Weise, 1899 =) *gentilis* (Erichson, 1847).
   Miocolaspis Spaeth, 1914*c* : 31 (*errore*).
3. *Agenysa* Spaeth, 1905 : 90, *Cassida caedemadens* Lichtenstein, 1796, by original designation.
   Agempa Spaeth, 1919 : 192 (*err. typ.*).

Tribe 12. **Stolaini** (*Elytrogonites* Chapuis, *Chelymorphites* Chapuis, *Omoplatites* Chapuis, *Mesomphaliites* Chapuis *partim*, *Mesomphaliitae* Spaeth).

1. *Stolas* Billberg, 1820 : 58, *Cassida* (*discors* Fabricius, 1801 =) *discoides* Linnaeus, 1758, by designation of Barber and Bridwell, 1940 : 9–10.
   Pseudomesomphalia Spaeth, 1901*b* : 338, *Cassida discors* Fabricius, by designation of Barber and Bridwell, 1940 : 9.
   Championaspis Spaeth, 1913*c* : 133, monobasic, *Mesomphalia nigrolineata* Champion, 1893 (**syn. n.**).
   Hadraspis Spaeth, 1915*c* : 279, monobasic, *H. helleri* Spaeth, 1915 (**syn. n.**).

a. *Cyrtonota* Chevrolat *in* Dejean, 1837 : 368, 392, *Cassida lateralis* (Fabricius =) Linnaeus, 1758, by designation of Duponchel and Chevrolat *in* D'Orbigny, 1843 : 211. (Subgenus).
   Neomphalia Spaeth, 1913*c* : 131, *Cassida lateralis* Linnaeus, by designation of Barber and Bridwell, 1940 : 9.
   Semaia Spaeth, 1909*b* : 370, monobasic, *S. compulsa* Spaeth, 1909.

b. *Mesomphalia* Hope, 1839 : 94, *Cassida gibbosa* Fabricius, 1781, by original designation. (Subgenus.)

- c. *Trilaccodea* Spaeth, 1902*a* : 98, monobasic, *T. langei*, Spaeth 1902. (Subgenus).
- d. *Anacassis* Spaeth, 1913*c* : 139, *Cassida fuscata* Klug, 1829, by original designation. (Subgenus).
- e. *Nebraspis* Spaeth, 1913*c* : 134, *Poecilaspis corticina* Boheman, 1850, by original designation. (Subgenus).
- f. *Xenicomorpha* Spaeth, 1913*c* : 137, monobasic, *Omoplata scapularis* Boheman, 1854. (Subgenus).
- g. *Botanochara* Dejean, 1837 : 369, 393, *Cassida* (*nervosa* Fabricius 1801 =) *impressa* Panzer *in* Voet, 1798, by present designation. (Subgenus).
  - *Poecilaspis* Hope, 1840 : 159, 160, *Cassida sedecim-pustulata* Fabricius, 1781, by original designation. (*Paecilaspis* err. typ.)
- h. *Poecilaspidella* Spaeth, 1913*c* : 135, *Poecilaspis proxima* Boheman, 1850, by original designation. (Subgenus).

2. *Eutheria* Spaeth, 1909*a* : 723, monobasic, *Chelymorpha piperata* Burmeister, 1870.
3. *Anepsiomorpha* Spaeth, 1913*c* : 135, monobasic, *Poecilaspis deplanata* Boheman, 1850.
4. *Hilarocassis* Spaeth, 1913*c* : 133, *Cassida exclamationis* Linnaeus, 1767, by present designation.
5. *Zatrephina* Spaeth, 1909*a* : 720, *Chelymorpha imperialis* Guérin-Méneville 1844, by original designation.
6. *Terpsis* Spaeth, 1913*c* : 132, monobasic, *Mesomphalia quadrivittata* Champion, 1893.
7. *Elytrogona* Chevrolat *in* Dejean, 1837 : 370, 394, monobasic, *Cassida* (*ampulla* Olivier, 1808 =) *quattuordecim-maculata* Latreille, 1802.
   - *Cyphoptera* Hope, 1840 : 160, monobasic, *C. ampulla* Olivier.
8. *Stoiba* Spaeth, 1909*a* ; 720, *Cassida flavicollis* Klug, 1829, by original designation.
9. *Amythra* Spaeth, 1913*c* : 135, *Coptocycla valida* Boheman, 1855, by designation of Spaeth, 1914*c* : 48.
10. *Paraselenis* Spaeth, 1913*c* : 138, *Cassida axillaris* Sahlberg, 1823, by present designation.
    - a. *Pseudechoma* Spaeth, 1913*c* : 139, monobasic, *Omoplata marginipennis* Spaeth, 1907. (Subgenus).
    - b. *Spaethiechoma* Hincks, 1950*a* : 511, new name for *Echoma* Spaeth, 1913, *nec* Chevrolat, 1837. (Subgenus).
      - *Echoma* Spaeth, 1913*c* : 138, *Cassida flava* Linnaeus, 1758, by original designation.
11. *Ogdoecosta* Spaeth, 1909*a* : 718, *Chelymorpha juvenca* Boheman, 1854, by present designation.
12. *Chelymorpha* Chevrolat *in* Dejean, 1837 : 369, 393, *Cassida multipunctata* Olivier, 1790, by designation of Duponchel and Chevrolat *in* D'Orbigny, 1843 : 211.
    - *Cyphomorpha* Hope, 1840 : 160, *Cassida* (*gibba* Fabricius, 1798 =) *variolosa* Olivier, 1790, by original designation.
13. *Phytodectoidea* Spaeth, 1909*a* : 718, *Chelymorpha quattuordecim-punctata* Boheman, 1854, by present designation.

14. *Echoma* Chevrolat *in* Dejean, 1837 : 370, 394, *Cassida marginata* (Fabricius =) Linnaeus, 1767, by designation of Duponchel and Chevrolat *in* D'Orbigny, 1843 : 211.
    Omoplata Hope, 1840 : 158, 159, *Cassida marginata* Linnaeus, by original designation.
    a. **Pseudomoplata** Spaeth, subgen. n. (p. 344), *Omoplata weyenberghi* Dohrn, 1878, by present designation. (Subgenus).
15. *Acromis* Chevrolat *in* Dejean, 1837 : 370, 394, monobasic, *Cassida spinifex* (Fabricius =) Linnaeus, 1763.
    Selenis Hope, 1840 : 160, *Cassida* (*perforata* Pallas = Fabricius) *spinifex* Linnaeus, by original designation.
16. *Omaspides* Chevrolat *in* Dejean, 1837 : 371, 395, *Cassida* (*transversa* Fabricius =) *clathrata* Linnaeus, 1758, by designation of Hope, 1840 : 158.
    Omaspides Boheman, 1854 : 144, *Cassida clathrata* Linnaeus, by designation of Spaeth, 1914*c* : 55.
    a. *Parechoma* Spaeth, 1913*c* : 136, monobasic, *Omoplata semilineata* Boheman, 1854. (Subgenus).
    b. *Paromaspides* Spaeth, 1913*c* : 139, *Omoplata sobrina* Boheman, 1854, by original designation. (Subgenus).

Tribe 13. **Ischyrosonychini** (*Ischyrosonychites* Chapuis, *Ischyrosonycitae* Spaeth).
1. *Ischyrosonyx* Sturm, 1843 : 273, monobasic, *Cassida* (*oblonga* Thon, 1826–28, *nec* Illiger, 1798 =) *thoni* Barber, 1946.
    Eurypedus Gistel, 1834, Barber, 1946*a* : 290.
2. *Cistudinella* Champion, 1893 : 164, monobasic, *C. foveolata* Champion, 1893.

Tribe 14. **Asterizini** (*Cassidites* Chapuis *partim*, *Asterizitae* Spaeth).
1. *Asteriza* Chevrolat *in* Dejean, 1837 : 372, 396, monobasic, *Cassida flavicornis* Olivier, 1790.

Tribe 15. **Physonotini** (*Cassidites* Chapuis *partim*, *Physonotitae* Spaeth).
1. *Physonota* Boheman, 1854 : 190, *P. alutacea* Boheman, 1854, by present designation.
    a. **Physonaspis** Spaeth, subgen. n. (p. 345), monobasic, *Omoplata calcarata* Boheman, 1854. (Subgenus).
    b. *Platycycla* Boheman, 1854 : 240, monobasic, *P. deruta* Boheman, 1854. (Subgenus).
    c. *Eurypepla* Boheman, 1854 : 236, *Cassida jamaicensis* Linnaeus, 1758, by present designation. (Subgenus).
    d. *Enagria* Spaeth, 1913*c* : 139, *Physonota ovata* Boheman, 1854, by original designation. (Subgenus).

Tribe 16. **Aspidomorphini** (*Aspidomorphites* Chapuis *partim*, *Aspidomorphitae* Spaeth).
1. *Aspidomorpha* Hope, 1840 : 158, *Cassida miliaris* Fabricius, 1775, by original designation.
    Iphinoë Spaeth, 1898 : 540, monobasic, *I. ganglbaueri* Spaeth, 1898.
    Spaethia Berg, 1899 : 79, new name for *Iphinoë* Spaeth, *nec* Bate, 1856.
    a. *Megaspidomorpha* Spaeth, 1943 : 48, *Cassida chlorotica* Olivier, 1808, by present designation. (Subgenus).

b. *Weiseocassis* Spaeth, 1932*a* : 3, *Aspidomorpha prasina* Weise, 1899, by original designation. (Subgenus).
c. *Conchyloctenia* Spaeth, 1902*b* : 449, *Cassida hybrida* Boheman, 1854, by designation of Maulik, 1919 : 339. (Subgenus).
2. *Mahatsinia* Spaeth, 1919 : 191, monobasic, *Laccoptera nodulosa* Weise, 1910.
3. *Nilgiraspis* Spaeth, 1932*a* : 2, monobasic, *Aspidomorpha andrewesi* Spaeth, 1914.
4. *Sindia* Weise, 1897 : 105, monobasic, *Cassida* (*clathrata* Fabricius 1798, *nec* Linnaeus, 1758 =) *sulcata* Olivier, 1808.
5. *Sindiola* Spaeth, 1903 : 111, monobasic, *S. parallelipennis* Spaeth, 1903.
6. *Hybosinota* Spaeth, 1909*c* : 282, *Cassida nodulosa* Boheman, 1854, by present designation.
7. *Laccoptera* Boheman, 1855 : 55, *L. excavata* Boheman, 1855, by designation of Maulik, 1919 : 346.
Parorphnoda Spaeth, 1932*a* : 228, *L. excavata* Boheman, by original designation. (*Parophnoda* Spaeth, *err. typ.*)
a. *Patrisma* Fairmaire, 1891 : 272, monobasic, *P.* (*pyramidalis* Fairmaire, 1891 =) *murrayi* (Boheman, 1862). (Subgenus).
b. *Orphnoda* Weise, 1899*a* : 247, 252, *Laccoptera cancellata* Boheman, 1855, by present designation. (Subgenus).
c. *Orphnodina* Spaeth, 1932*a* : 229, *Laccoptera distans* Spaeth, 1902, by present designation. (Subgenus).
d. *Asphalesia* Weise, 1899*a* : 246, 247, *A. confragosa* Weise, 1899, by designation of Spaeth, 1914*c* : 82. (Subgenus).
e. *Orphnodella* Spaeth, 1902*c* : 20, *Laccoptera* (*rubiginosa* Weise, 1899, *nec* Boheman, 1855 =) *abyssinica* (Boheman, 1856) by present designasignation. (Subgenus).
f. **Indocassis** Spaeth, subgen. n. (p. 345), *Cassida foveolata* Boheman, 1856, by present designation. (Subgenus).
g. **Laccopteroidea** Spaeth, subgen. n. (p. 345), *Cassida tredecim-punctata* Fabricius, 1801, by present designation. (Subgenus).
h. **Eulaccoptera** Hincks, *nom. nov. pro Laccoptera* s.str. Spaeth, 1932*a* : 229, (*nec* Boheman), *Cassida corrugata* Sahlberg, 1823, by present designation.

Tribe 17. **Basiptini** (*Basiptites* Chapuis, *Basiptitae* Spaeth).
1. *Basipta* Chevrolat *in* D'Orbigny, 1842 : 489, monobasic, *B. glauca* Chevrolat, 1842 (*stolida* Boheman, 1854).

Tribe 18. **Cassidini** (*Cassidites*, *Chiridites* Chapuis).

A. Old World Genera.

1. *Macromonycha* Spaeth, 1911 : 271, *Cassida apicalis* Gebler, 1845, by designation of Spaeth, 1914*c* : 88.
Kari Maulik, 1923 : 603, monobasic, *K. brunnea* Maulik, 1923 = *M. apicalis* aberr.
2. *Nabathaea* Spaeth, 1911 : 272, *N. pygmaea* Spaeth, 1911, by present designation.
3. *Chiridula* Weise, 1889*a* : 647, monobasic, *C. semenowi* Weise, 1889.

4. *Eremocassis* Spaeth, 1926*a* : 13, 15, monobasic, *E. transcaspica* Spaeth, 1926.
5. *Ischyronota* Weise, 1891 : 204, *Cassida desertorum* Gebler, 1833, by present designation.
6. *Oxylepis* Desbrochers, 1884 : 100, *Cassida deflexicollis* Boheman, 1862, by present designation. (*Oxylepus* in 1884, emend. Desbrochers 1891 to *Oxylepis*.)
   Chelysida Fairmaire 1882*b* : 103, *partim*.
   a. *Embolocassis* Spaeth, 1936*b* : 11, monobasic, *O.* (*E.*) *cuneipennis* Spaeth, 1936. (Subgenus).

6a. **Limnocassis** Spaeth, gen. n. (p. 346), monobasic, *Oxylepis turneri* Spaeth, 1933.

7. *Orobiocassis* Spaeth, 1934 : 392, *Cassida gabonicola* Spaeth, 1933, by original designation.
8. *Chelysida* Fairmaire, 1882*b* : 104, *C. obtecta* Fairmaire, 1882, by designation of Spaeth, 1914*c* : 86.
9. *Smeringaspis* Spaeth, 1924 : 312, *Cassida setifera* Boheman, 1854, by original designation.
   a. **Luimbelia** Spaeth, subgen. n. (p. 345), monobasic, *L. hirsuta* Spaeth, sp. n. (p. 346). (Subgenus).
10. *Trichaspis* Spaeth, 1911 : 269, monobasic, *Cassida pilosula* Boheman, 1862.
    a. *Crossocassis* Spaeth, 1911 : 274, monobasic, *C. pilosa* Spaeth, 1911. (Subgenus).
11. *Psalidoma* Spaeth, 1899 : 217, monobasic, *P. holubi* Spaeth, 1899.
12. *Sphenocassis* Spaeth, 1911 : 261, monobasic, *Laccoptera humerosa* Fairmaire, 1898.
    a. *Torbinia* Spaeth, 1911 : 262, monobasic, *T. incisicollis* Spaeth, 1911. (Subgenus).
13. *Acrocassis* Spaeth, 1924 : 312, *Cassida gibbipennis* Boheman, 1854, by original designation.
    Hypocassida Weise, 1903 : 224, *partim*.
14. *Silana* Spaeth, 1914*a* : 563, monobasic, *Cassida farinosa* Boheman, 1856.
15. **Capelocassis** Spaeth, gen. n. (p. 346), monobasic, *Cassida dorsata* Duvivier, 1891.
16. *Glyphocassis* Spaeth, 1914*a* : 547, monobasic, *Cassida trilineata* Hope, 1831.
17. *Hebdomecosta* Spaeth, 1915*b* : 361, *H. reitteri* Spaeth, 1915 (= *spilota* Gorham, 1885), by original designation.
18. *Ischiocassis* Spaeth, 1917 : 435, monobasic, *Cassida umbrata* Boheman, 1854.
19. *Fornicocassis* Spaeth, 1917 : 438, monobasic, *F. rufocincta* Spaeth, 1917.
20. *Oocassida* Weise, 1897 : 110, monobasic, *Cassida pudibunda* Boheman, 1856.

20a. *Andevocassis* Spaeth, 1924 : 310, monobasic, *Cassida nigroguttata* Fairmaire, 1904 (*nigropunctata* Spaeth, *lapsus* !).

21. *Tegocassis* Spaeth, 1924 : 310, *Cassida corpulenta* Weise, 1904, by original designation.

22. *Cassida* Linnaeus, 1758 : 362, *C. nebulosa* Linnaeus, 1758, by designation of Spaeth, 1914*b* : 140.[2]
   - a. *Lordicassis* Reitter, 1926 : 23, 27, monobasic, *Cassida undecimnotata* Gebler, 1833. (Subgenus).
   - b. *Cassidulella* Strand, 1928 : 2, new name for *Cassidula* Weise, 1889*b*, (*nec* de Blainville, 1830).
     Cassidula Weise, 1889*b* : 260, *Cassida nobilis* Linnaeus, 1758, by present designation. (Subgenus).
   - c. *Pseudocassida* Desbrochers, 1891 : 15, monobasic, *Cassida murraea* Linnaeus, 1768. (Subgenus).
   - d. *Mionycha* Weise, 1891 : 204, monobasic, *Cassida azurea* Fabricius, 1801. (Subgenus).
   - e. *Alledoya* Hincks, 1950*a* : 508, new name for *Deloyala* Redtenbacher, 1858, (*nec* Duponchel and Chevrolat, 1843).
     Deloyala Redtenbacher, 1858 : 952, *Cassida seraphina* Ménétriés, 1836, by designation of Hincks, 1950*a* : 508. (Subgenus).
   - f. *Tylocentra* Reitter, 1926 : 24, 57, *Cassida turcmenica* Weise, 1892, by present designation. (Subgenus).
   - g. *Lordiconia* Reitter, 1926 : 23, 26, monobasic, *Cassida canaliculata* Laicharting, 1781. (Subgenus).
   - h. *Hypocassida* Weise, 1893 : 1074, *Cassida subferruginea* Schrank, 1776, by present designation. (Subgenus).
   - i. *Odontionycha* Weise, 1891 : 204, *Cassida viridis* Linnaeus, 1758, by present designation. (Subgenus).
   - j. **Mionychella** Spaeth, subgen. n. (p. 346), *Cassida hemisphaerica* Herbst, 1799, by present designation. (Subgenus).
   - k. *Pilemostoma* Desbrochers, 1891 : 14, monobasic, *Cassida* (*vittata* Fabricius, 1798 =) *fastuosa* Schaller, 1783. (Subgenus).
   - l. *Taiwania* Spaeth, 1913*d* : 47, monobasic, *T. sauteri*, Spaeth 1913. (Subgenus).
   - m. *Onychocassis* Spaeth, 1926*a* : 23, 16, *Cassida brevis* Weise, 1884, by present designation. (Subgenus).
   - n. *Bassamia* Spaeth, 1924 : 312, monobasic, *Cassida paeminosa* Boheman, 1856. (Subgenus).
   - o. *Erbolaspis* Spaeth, 1924 : 312, monobasic, *Hypocassida passaria* Weise, 1900. (Subgenus).
   - p. *Trigonocassis* Hincks, 1950*a* : 512, new name for *Trigonaspis* Spaeth, 1924 (*nec* Hartig, 1840).
     Trigonaspis Spaeth, 1924 : 311, monobasic, *Cassida conducta* Boheman, 1862. (Subgenus).
   - q. **Chloocassis** Spaeth, subgen. n. (p. 347), monobasic, *Odontionycha indicola* Duvivier, 1892. (Subgenus).
   - r. *Rhytidocassis* Spaeth, 1941 : 316, monobasic, *Cassida limbiventris* Boheman, 1854. (Subgenus).

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[2] Several invalid designations have been made. Latreille, 1810 : 432 cited *C. equestris* Fabricius, 1787 ; Curtis, 1826 : 127 indicated *C. viridis* Fabricius, 1775, and Westwood, 1839 : 42 *C. murraea* Linnaeus, 1768. None of these names were actually originally included in the genus by Linnaeus, although *C. equestris* F. by subsequent synonymy is *C. viridis* Linnaeus, 1758.

23. *Aethiopocassis* Spaeth, 1924 : 315 (as subgenus), *Cassida vigintimaculata* Thunberg, 1789, by present designation.
24. *Chiridopsis* Spaeth, 1924 : 337, *Coptocycla aubei* Boheman, 1855, by original designation.
    Chirida (Chapuis) Weise, 1896*a* : 12 (*partim*).
25. *Thlaspida* Weise, 1899*b* : 272, *Coptocycla cribrosa* Boheman, 1855, by designation of Spaeth, 1914*c* : 127.
26. *Thlaspidula* Spaeth, 1901*a* : 9, monobasic, *T. fimbriata* Spaeth, 1901.
    Elpinora Spaeth, 1903 : 119, monobasic, *E. mülleri* Spaeth, 1903.
27. *Thlaspidosoma* Spaeth, 1901*a* : 4, *T. dohrni* Spaeth, 1901, by designation of Spaeth, 1914*c* : 128.
    Crepidaspis Spaeth, 1912*a* : 119, monobasic, *C. varicornis* Spaeth, 1912.
28. *Meroscalsis* Spaeth, 1903 : 113, *Coptocycla radiata* Boheman, 1855, by original designation.
    a. *Melichrocassis* Spaeth, 1913*a* : 451, *M. blackburni* Spaeth, 1913, by present designation. (Subgenus).
29. *Rhacocassis* Spaeth, 1904 : 76, monobasic, *Coptocycla flavoplagiata* Baly, 1863.
30. *Thlaspidomorpha* Spaeth, 1914*a* : 563, monobasic, *Coptocycla balyi* Boheman, 1855.
31. *Lorentzocassis* Spaeth, 1913*a* : 449, monobasic, *L. papuana* Spaeth, 1913.
    Lorentzia (*Lorentsia err. typ.*), Spaeth, 1912*a* : 120 (*nec* Cameron, 1911), monobasic, *L. purpurascens* Spaeth, 1912.
32. **Malayocassis** Spaeth, gen. n. (p. 347), *Coptocycla hilaris* Boheman, 1855, by present designation.
33. *Emdenia* Spaeth, 1915*a* : 236, monobasic, *Chirida maxima* Blackburn, 1896.
34. *Austropsecadia* Hincks, 1950*a* : 508, new name for *Psecadia* Weise, 1900.
    Psecas Weise, 1899*b* : 272, monobasic, *P. chlorina* Weise, 1899 (*nec* Koch, 1850).
    Psecadia Weise, 1900*a* : 458, new name for *Psecas* Weise, *nec* Koch.
35. **Hovacassis** Spaeth, gen. n. (p. 347), *Coptocycla discolor* Boheman, 1855, by present designation.

B. **New World Genera.**

36. *Rhoia* Spaeth, 1913*c* : 144, monobasic, *R. clavareaui* Spaeth, 1913.
37. *Scaeocassis* Spaeth, 1913*c* : 141, monobasic, *Cassida combusta* Boheman, 1854.
38. *Hybosa* Duponchel and Chevrolat *in* D'Orbigny, 1842 : 256, *H. gibbera* Boheman, 1855, by present designation.
39. *Exestastica* Spaeth, 1909*a* : 721, monobasic, *Chelymorpha ignobilis* Boheman, 1854.
40. **Floridocassis** Spaeth, gen. n. (p. 348), monobasic, *Cassida repudiata* Suffrian, 1868.
41. *Mexicaspis* Spaeth, 1936*a* : 259, monobasic, *Coptocycla azteca* Champion, 1894.

42. *Jonthonota* Spaeth, 1913*c* : 141, *Cassida nigripes* Olivier, 1790, by original designation.
43. *Erepsocassis* Spaeth, 1936*a* : 260, monobasic, *Coptocycla rubella* Boheman, 1862.[3]
44. *Strongylocassis* Hincks, 1950*a* : 511, new name for *Strongylaspis* Spaeth, 1936*a*, (*nec Strongylaspis* J. Thompson, 1860).
    [4]*Strongylaspis* Spaeth, 1936*a* : 216, 259, monobasic, *Coptocycla bisignata* Boheman, 1855.
45. *Chersinellina* Hincks, 1950*a* : 509, new name for *Chersinella* Champion, 1894 (*nec* Gray, 1870).
    Chersinella Champion, 1894 : 175, monobasic, *Cassida heteropunctata* Boheman, 1854.
46. **Chacocassis** Spaeth, gen. n. (p. 348), monobasic, *Coptocycla fuscovittata* Boheman, 1855.
47. *Saulaspis* Spaeth, 1913*c* : 143, *Cassida bistrilineata* Boheman, 1854, by present designation.
48. **Aporocassida** Spaeth, gen. n. (p. 348), monobasic, *Cassida graphica* Germar, 1824.
49. *Agroiconota* Spaeth, 1913*c* : 142, *Cassida tristriata* Fabricius, 1792, by original designation.
50. *Gratiana* Spaeth, 1913*c* : 142, *Cassida spadicea* Klug, 1829, by original designation.
51. *Parorectis* Spaeth, 1901*b* : 346, *Cassida callosa* Boheman, 1854, by original designation. (Described as subgenus).
    Orectis Spaeth, 1901*b* : 346, *Cassida rugosa* Boheman, 1854, by original designation (*nec* Lederer, 1857).
52. *Crambelea* Spaeth, 1913*c* : 143, monobasic, *Batonota illudens* Boheman, 1854.
53. *Cyclocassis* Spaeth, 1913*c* : 143, monobasic, *Coptocycla circulata* Boheman, 1855.
54. **Leptocodia** Spaeth, gen. n. (p. 348), monobasic, *Coptocycla luctifera* Boheman, 1855.
55. *Ischnocodia* Spaeth, 1942 : 34, monobasic, *Cassida annulus* Fabricius, 1781.
56. **Aidoia** Spaeth, gen. n. (p. 349), monobasic, *Coptocycla nubilosa* Boheman, 1855.
57. *Orexita* Spaeth, 1911 : 254, *Coptocycla complanata* Boheman, 1855, by present designation.
58. *Coptocycla* Chevrolat, 1837 : 372, 396, *Cassida undecim-punctata* Fabricius, 1781, by designation of Duponchel and Chevrolat, *in* D'Orbigny, 1843 : 211.
    Thyreaspis Hope, 1840 : 158, 159, *Cassida undecim-punctata* Fabricius, by original designation.
    a. **Coptocyclella** Hincks, subgen. n. (p. 349), *Cassida adamantina* Germar, 1824, by present designation. (Subgenus.)

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[3] This genus is considered to be a synonym of *Metriona* Weise by Sanderson and King (1951, *J. Kansas ent. Soc.* **24** : 126).

[4] Regarded as a synonym of *Metriona* Weise by Sanderson and King (see footnote No. 3).

b. *Dyscineta* Spaeth, 1936*c* : 252, 260, monobasic, *D. robusta* Spaeth, 1936. (Subgenus).

c. *Psalidonota* Boheman, 1855 : 81, *P. contemta* Boheman, 1855, by present designation. (Subgenus).

d. *Podostraba* Spaeth, 1936*c* : 253, 259, *Cassida arcuata* Swederus, 1787, by original designation. (Subgenus).

59. *Nuzonia* Spaeth, 1912*b* : 5, *N. ibaguensis* Spaeth, 1912, by present designation.

Litocassis Weise, 1921 : 197, monobasic, *L. placidula* Weise, 1921 = *N. gestatrix* (Boheman, 1855).

60. *Plagiometriona* Spaeth, 1899 : 220, *Coptocycla vigens* Boheman, 1855, by present designation. (Subgenus).

a. *Parametriona* Spaeth, 1937 : 143, 144, *Coptocycla ambigena* Boheman, 1855, by original designation. (Subgenus).

61. *Metriona* Weise, 1896*a* : 13, 14, *Cassida elatior* Klug, 1829, by designation of Spaeth, 1914*c* : 136.

62. **Bradycassis** Spaeth, gen. n. (p. 349), *Coptocycla drewseni* Boheman, 1855, by present designation.

63. *Parachirida* Spaeth, 1942 : 38, *Coptocycla semiannulata* Boheman, 1855, by present designation.

64. *Deloyala* Chevrolat, 1837 : 371, 395 *Cassida cruciata* Linnaeus, 1758, by designation of Duponchel and Chevrolat *in* D'Orbigny, 1843 : 211 (as *C. crux* Fabricius, 1781).

Chirida Chapuis, 1875 : 405, *Cassida cruciata* Linnaeus, by designation of Weise, 1896*a* : 14.

65. *Syngambria* Spaeth, 1911 : 275, *Coptocycla andreae* Boheman, 1855, by present designation.

66. **Helocassis** Spaeth, gen. n. (p. 349), monobasic, *Coptocycla flexuosa* Boheman, 1855.

67. *Charidotella* Weise, 1896*a* : 13, monobasic, *Cassida zona* Fabricius, 1801 (described as subgenus).

a. *Philaspis* Spaeth, 1913*c* : 142, *Odontionycha seriatopunctata* Spaeth, 1901, by present designation. (Subgenus).

b. **Chaerocassis** Spaeth, subgen. n. (p. 350), *Coptocycla marculenta* Boheman, 1855, by present designation. (Subgenus).

c. *Xenocassis* Spaeth, 1936*a* : 260, *Coptocycla amoena* Boheman, 1855, by original designation. (Subgenus.)

68. *Metrionella* Spaeth, 1932*b* : 263, *Coptocycla erratica* Boheman, 1855, by original designation.

69. **Tetracassis** Spaeth, gen. n. (p. 350), monobasic, *Metriona lyra* Spaeth, 1898.

70. *Tapinaspis* Spaeth, 1936*a* : 260, *Coptocycla wesmaeli* Boheman 1855, by original designation.

71. *Drepanocassis* Spaeth, 1936*a* : 262, *Coptocycla profana* Boheman, 1855, by original designation.

72. *Metrionaspis* Spaeth, 1942 : 39, monobasic, *Aspidomorpha rubicunda* Guérin-Méneville, 1844.

Tribe 19. **Charidotini** (*Aspidomorphites* Chapuis *partim*, *Charidotitae* Spaeth).

1. *Charidotis* Boheman, 1854 : 152 ; 1855 : 7, *C. miniata* Boheman, 1855, by present designation.
2. *Ctenocharidotis* Spaeth, 1926*b* : 9, 21, *Coptocycla crispata* Boheman, 1855, by present designation.
3. *Cteisella* Weise, 1896*a* : 15, *Coptocycla virescens* Boheman, 1855, by designation of Spaeth, 1914*c* : 149.
   a. *Ctenocassida* Spaeth, 1926*b* : 11, *Coptocycla vittigera* Boheman, 1855, by present designation. (Subgenus).
4. *Pseudoctenochira* Spaeth, 1926*b* : 5, monobasic, *P. octo-lineata* Spaeth, 1926.
5. *Ctenophilaspis* Spaeth, 1926*b* : 5, monobasic, *Coptocycla ingenua* Boheman, 1855.
6. *Microctenochira* Spaeth, 1926*b* : 36, 104, *Coptocycla jousselini* Boheman, 1855, by original designation.
   a. *Euctenochira* Hincks, 1950*a* : 509, new name for *Ctenochira* Chapuis, 1875 (*nec* Foerster, 1855).
      Ctenochira Chapuis, 1875 : 409, *Coptocycla aciculata* Boheman, 1855, by designation of Weise, 1896*a* : 14. (Subgenus).

4. DESCRIPTIONS OF NEW GENERA, SUBGENERA AND SPECIES.

Pseudandroya Spaeth, gen. n.

Von den ihr äusserlich ähnlichen Arten der Gattung *Androya* durch unter dem Prosternum verstreckte Mundteile sowie nicht gestielte Augen verschieden ; durch die lange, schmale Körperform erinnert *Pseudandroya* an *Calopepla*.

Fühler kurz, vom 7. Gliede an dicht und fein längsrissig, die Basalglieder, mit Ausnahme des 1., so lang als breit, die Endglieder flachgedrückt, bis zum vorletzten in der Dicke zunehmend, kürzer als ihre grösste Breite. Kopfschild kurz dreieckig, Halsschild trapezförmig, vorn nicht ausgerandet, mit stumpfwinkligen Vorder- und etwas eingezogenen Hinterecken, an den Seiten und vorn mit Ausnahme der Mitte dick gerandet, die Basis ebenso wie die der Flügeldecken mit kräftiger Krenulierung ; letztere nach hinter kaum erweitert, mit 10 nicht ganz regelmässigen, groben Punktstreifen und 4 wenig überhöhten primären Zwischenräumen ; Seitendach schmal, Prosternum flach, breit, der Fortsatz nicht erweitert. Oberseite braun, Fühler und Beine schwarz, Unterseite und Epipleuren rotbraun, die Brust hinter dunkler.

Monobasic, *Calopepla livingstonei* Baly, 1864.

Spaethaspis Hincks, gen. n.

Antennae probably 11-segmented (segments beyond ninth missing in type) ; two proximal segments hairless, the following segments feebly pubescent and cylindrical in shape, being of the same width at either extremity ; second segment about half as long as first or third, fourth as long as third, the rest becoming progressively shorter. Clypeus very short, nearly four times as broad as long ; vertex deeply impressed. Prosternum broad, strongly expanded behind with deep longitudinal grooves, the middle of which being longest and broadest. Pronotum with caudal margin prominent and more or less truncate adjacent to scutellum, slightly oblique on either side to rectangular caudal angles ; sides straight in basal two-thirds, slightly converging towards the front, where they are broadly rounded; cephalic margin deeply emarginate mesad with a pore and bristle at the outer angles. Elytra moderately broad, almost twice as long as broad, with finely punctured striae separated by broad interstices ; behind shoulders is a transverse impression ; lateral areas rather narrow, somewhat concave with polished margin. Claws with large basal tooth.

Type : *Spaethaspis lloydi* sp. n.

Spaethaspis lloydi Hincks, sp. n.

Underside, antennae, head and pronotum reddish-testaceous ; legs, scutellum and lateral areas of elytra testaceous ; disc of latter blue-black.

Vertex feebly and diffusely punctured. Pronotum transverse, diffusely punctured, rather finely and feebly on disc, strongly and distinctly at sides ; caudal angles with shallow depression. Elytra slightly widened behind, broadly rounded at apex ; striae finely and closely punctured ; interstices about four times as broad as striae, very indistinctly punctured. Abdominal sternites flat, very finely punctured ; last segment more or less truncate, without emargination. Length 9 × 6 mm.

ECUADOR : Type in Manchester Museum (Spaeth Collection). Named after R. W. Lloyd, Esq.

This species was separated by Dr. Spaeth and described in manuscript under an invalid generic name. The genus belongs to a tribe (the Imatidiini) which stands on the borderline between the Hispinae and the Cassidinae. From the little that is known of their habits and larvae it is possible that the tribe may have to be transferred to the former subfamily eventually.

Chlamydocassis Spaeth, gen. n.

Weise hat in *Dtsch. ent. Z.* 1900 : 460 von Boheman's Gattung *Desmonata* jene Arten abgetrennt, die statt 6 nur 4 oder 5 glänzende Basalglieder haben und deren Prosternum schmal und zwischen den Hüften verengt ist ; für diese Arten errichtete er unter Verwendung des alten Dejean'schen Namens die Gattung *Polychalca*,[5] wobei er als Typus die *Cassida multicava* Latreille bezeichnete ; leder weicht gerade diese Art von allen anderen zu *Polychalca* gestellten so sehr ab, dass eine Trennung nötig ist ; dabei muss natürlich der Name bei der von Weise als Gattungstypus vorgeschlagenen Art verbleiben ; für die anderen schlage ich den Namen *Chlamydocassis* vor. Für diese gelten folgende Merkmale : Fühler mässig lang, mit 3 oder 4 von den Engliedern nicht immer scharf getrennten Basalgliedern, die Endglieder nicht rundlich meist um die Hälfte breiter als lang. Prosternum mässig breit, gewöhnlich mit einer Grube. Halsschild vorn ausgerandet, die Mitte der Ausrandung häufig schwach vorgezogen. Ober und Unterseite metallisch. Verbreitung : Südamerika. Gattungstypus : *Cassida metallica* Klug, 1829.

Pseudomoplata Spaeth, subgen. n.

Von *Omoplata* hauptsächlich durch die Halsschildform verschieden ; er ist trapezförmig, seine Seiten gehen anfangs senkrecht von der Basis weg, dann laufen sie schräg nach vorn, wo der Halsschild breit abgestutzt ist, so dass Scheitel und Augen von oben sichtbar sind ; die Basis ist jederseits ausgerandet und die Hinterecken treten zähnchenförmig nach hinten aus. Fühler mit 4 basalen, von den Endgliedern scharf getrennten Gliedern, das 3. länger als das 4., die Endglieder nur wenig länger als dick. Prosternum flach, fast ohne Eindruck. Klauenzahn ziemlich gross. Das Seitendach ist beim ♂ vorn breiter, hat an der Schulter ein Zähnchen und innen davon eine Ausrandung.

Typus : *Omoplata weyenberghi* Dohrn, 1878.

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[5] As indicated on p. 333, Weise's interpretation of this genus, followed by Spaeth, was incorrect. *Polychalca* Weise (*nec* Chevrolat) has been renamed *Polychalma* by Barber and Bridwell, 1940 : 8, 9.

Physonaspis Spaeth, subgen. n.

Der Vorderrand der Vorderschienen ist am Ende erweitert, mehr oder minder dornförmig nach aussen ausgezogen ; Halsschild viel schmäler als die Basis der Flügeldecken, etwa halbkreisförmig, vorne viel mehr als hinten gerundet, kurz vor der Basis in den breit abgerundeten Hinterecken am breitesten, die Scheibe mit 3 länglichen, schwarzen Flecken vor der Basis ; Flügeldecken mit abgerundeten, nicht oder kaum vorgezogenen Schulterecken und verworrener Punktierung von Scheibe und Seitendach. Fühler mit 5 Basal- und wenig dickeren Endgliedern, die kaum länger als dick sind, unter den basalen ist das 2. das kürzeste, das 3. das längste. Oberlippe gewölbt, vorn tief ausgerandet. Kopfschild etwa so lang als breit, mit breitem, vorn zugespitztem und in die Fühlerbasis aufgebogenem Mittelfeld.

Typus : *Physonota calcarata* Boheman, 1854.

Indocassis Spaeth, subgen. n.

Der Vorderrand des Prosternums ist an der Seite tief und kurz eingeschnitten, seine Kante ist vorne weniger hoch als hinten vor dem Einschnitt ; an der Unterseite des Halsschildes ist hinter der Ausrandung eine geglättete Fläche, innen von einer dünnen Leiste begrenzt, zum Anlegen der Endglieder der Fühler. Das 2. Fühlerglied ist sehr kurz, das 3. mehr als doppelt so lang, länger als die folgenden Glieder. Kopfschild mit dreieckigem über die Fühlerbasis hoch ragendem, grubig punktiertem Mittelfeld. Halsschild halbkreisförmig, an der Basis am breitesten. Flügeldecken mit (gleichfarbiger) wenig erhabener Netzung, die die Punktstreifen unterbricht, gleichmässig gewölbt. Klauen nur innen mit Kammzähnen.

Typus : *Cassida foveolata* Boheman, 1856.

Laccopteroidea Spaeth, subgen. n.

Fühler ziemlich lang, mit 6 Basal- und 5 wenig dickeren Endgliedern, das 3. das längste, doppelt so lang als das 2. und länger als eines der folgenden, meist allmählich kürzeren Basalglieder ; Vorderrand des Prosternums in der Mitte nicht vorgezogen, an der Seite mit gleichmässigem Abfall. Kopfschild mit dreieckigem, über die Fühlerbasis ansteigendem Mittelfeld. Halsschild immer schmäler als die Basis der Flügeldecken, elliptisch oder nach vorn etwas erweitert, die abgerundeten Ecken dem gemäss in oder wenig vor der Mitte, die Scheibe längsrissig oder fein punktiert. Flügeldecken subtriangulär, mit Punktstreifen, der 1. primäre Zwischenraum immer höher, mehr oder minder rippenförmig, mit der Höckerstelle durch eine wenig nach hinten gerichtete Leiste verbunden, die folgenden primären Zwischenräume weniger, selten gar nicht uberhöht ; die Profillinie schwach gebrochen, hinten nicht oder sehr wenig ausgerandet. Die Klauen haben innen lange Kammzähne, aussen fehlen diese oder sind undeutlich.

Typus : *Cassida tredecim-punctata* Fabricius, 1801.

Luimbelia Spaeth, subgen. n.

Die Basalglieder der Fühler sind länger, das 3. um die Hälfte länger als das 2. und das diesem gleiche 4., das 5. und 6. sind noch länger, die Endglieder weniger verdickt als bei *setifera* Boh. [*Smeringaspis* s. str.] aber noch immer breiter als lang, nur das letzte lang, bis über seine Mitte verbreitert, dann zugespitzt. Stirn-linien weniger tief als in der vorigen Untergattung [*Smeringaspis* s. str.], vorn vom Augenrande entfernt. Die Ecke am Vorderande des Prosternums ist viel kleiner und stumpfer. Der Kopf ist in eine Höhlung der Halsschild-Unterseite eingebettet, so dass neben ihm eine undeutliche, aussen von einer Falte begrenzte Fühlerrinne ist. Umriss fast gerundet, viel breiter und verhältnismässig kürzer als bei *setifera*, das Seitendach ist breiter, weniger geneigt. Die Beborstung der Oberseite ist ungleich, die Punktstreifen sind nirgends verworren.

Typus *S.* (*L.*) *hirsuta* sp. n.

This subgenus is described in comparison with *Smeringaspis* Spaeth, s. str.

Smeringaspis (Luimbelia) hirsuta Spaeth, sp. n.

Breit eiförmig-gerundet, mässig gewölbt, matt, oben und unten behaart, die weissen Börstchen auf den Flügeldecken länger, auf Halsschild und Unterseite kürzer, oben dunkelbraun, das Vor und Seitendach wenig heller, unten schwarz, das 2. bis 6. Fühlerglied, die Knien, Schienen und Tarsen gelbbraun. Kopfschild mit halb verloschener Punktierung. Halsschild innen mit gerader, aussen bis zur Längsmitte vorgezogener Basis und abgestumpften Ecken. Die weissen Börstchen sind am Rande länger als auf der Scheibe. Flügeldecken so breit als der Halsschild, an der Seite kaum erweitert, an der Basis gerade abgestutzt, hinten verrundet. Die Punktstreifen sind grob, fast rinnenförmig vertieft, regelmässig, ihre Zwischenräume nur wenig breiter, gewölbt und mit weissen, nach hinten gekrümmten Börstchen besetzt, die auf den ersten zweien länger sind. Das Basaldreieck ist kaum eingedrückt, seine Kanten und mehrere Querleistchen unterbrechen die zwei ersten Streifen ; auch in der äusseren Hälfte sind einige überhöhte Querleisten, die zwischen den zwei letzten Streifen beulenförmig werden und sich auf das Seitendach fortsetzen, das hierdurch uneben erscheint. Epipleuren bis zur Spitze breit, mit sehr langen, weissen, abstehenden Haaren besetzt. Grösse : 5 × 4 mm. Angola : Luimbale, Mt. Moco 1,800–1,900 m., iii.1934 (ex coll. K. Jordan). Type in Spaeth collection, Manchester Museum. Von *S. setifera* Boh. durch breitere Körperform, stumpfe Ecke des Prosternums, längere, dünnere Fühler und andere Massverhältnisse der einzelnen Glieder, ferner durch ungleichmässige, zum Teil längere Behaarung, andere Art der Punktstreifen verschieden.

Limnocassis Spaeth, gen. n.

Das Klauenglied ist kurz, ragt wenig oder nicht über die Borstenkränze hinaus ; die Klauen sind ungezähnt ; Unterseite der Tarsenglieder fast immer mit filziger Behaarung. An der Unterseite des Halsschildes ist weder eine Fühlerrinne, noch eine Leiste oder Falte. Die Vorderrand des Prosternums fällt gleichmässig ab. Flügeldecken mit Punktstreifen, das Seitendach vorn viel schmäler als eine Decke der Scheibe ; Halsschild nach vorn verengt ; Körper viel länger als breit. Punktstreifen grob und tief, mit gewölbten Zwischenräumen, die primären schwach rippenförmig, besonders hinten überhöht ; zwischen Scheibe und Seitendach ist vor der Mitte eine Grube ; Schildchen breit abgerundet ; das 3. Fühlerglied ist kürzer als das 2. ; Halsschild wenig breiter als lang, mit verrundeten Ecken hinter der Mitte ; Seitendach zwar steil, aber von oben sichtbar, die schwach spitzwinkligen Ecken etwas vorgezogen.

Typus : *Oxylepis turneri* Spaeth, 1933.

Capelocassis Spaeth, gen. n.

Umriss trapezförmig, am Ende breit abgerundet ; Fühler kurz, mit 5 viel dickeren Endgliedern, deren mittlere breiter als lang sind ; das 2. bis 6. Glied nicht länger als dick, besonders das 3. und 4. kürzer als das zweite. Der Vorderrand des Prosternums fällt an der Seite gleichmässig ab. Kopfschild trapezförmig, flach, mit verloschenen Stirnlinien ; Halsschild vorne stark gerundet, die Basis aussen vorgezogen, die Ecken nahe der Längsmitte ; Flügeldecken im Basaldreieck tief eingedrückt, mit einem stumpfen Höcker, regelmässigen Punktstreifen und rippenförmigem primären ersten Zwischenraum, der durch eine Querleiste mit dem Höcker verbunden ist ; die mit einem kleinen, spitzigen Zahn versehenen Klauen überragen wenig die Borstenkränze.

Typus : *Cassida dorsata* Duvivier, 1891.

Mionychella Spaeth, subgen. n.

Die Klauen sind gezähnt. Die Ränder der Vor- und des Seitendaches sind nicht aufgebogen. Flügeldecken mit verworrener Punktierung. Die Stirnlinien des Kopfschildes konvergieren geradlinig ; das von ihnen umschlossene Mittelfeld ist schmäler dreieckig, flach ; die Basalglieder der Fühler sind zusammen viel kürzer als die Länge der Endglieder, das 3. Glied ist nur wenig, das 4. nicht länger als das zweite ; Seitendach steil, in der ganzen Länge von der Scheibe durch eine regelmässige, tiefere Punktreihe geschieden ; innen vorn ist ein breiterer Zwischenraum und ein gröberer Punktstreif ; Halsschild höchstens sehr wenig schmäler als die Basis der Flügeldecken.

Typus : *Cassida hemisphaerica* Herbst, 1799.

Chloocassis Spaeth, subgen. n.

Klauen mit einem grossen, rechtwinkligen Zahn ; der Vorderrand des Prosternums fällt an der Seite nach einer stumpfen Ecke steiler ab ; die Fühler sind kurz, das 3. Glied kürzer als das zweite, die drei folgenden kaum länger, die fünf Endglieder stark verdickt, davon das 7. mehr gestreckt, die anderen nicht länger als dick.

Eiförmig, vor der Mitte am breitesten, gleichmässig gewölbt ; Kopfschild fast quadratisch, vorn kaum schmäler, flach, mit undeutlichen, konvergierenden Stirnlinien ; Halsschild elliptisch, mit verrundeten Ecken etwas nach der Mitte. Flügeldecken mit verloschenen Rippen auf den zwei inneren primären Zwischenräumen und mit Ausnahme des Randstreifs, sowie der vorderen Hälfte des vorletzten Streifs stellenweise verworrener Punktierung. (Duvivier's Angabe : " profondément et reguliérement ponctuées," ist in diesem Sinne richtig zu stellen ; ex typo !).

Typus : *Odontionycha indicola* Duvivier, 1892.

Malayocassis Spaeth, gen. n.

Das besondere Merkmal dieser Gattung ist die Bildung der Oberlippe ; sie ist querelliptisch, mit abgerundeten, nicht scharfen Rändern ; die fein gekörnte Oberseite trägt einen scharfen Längskiel.

Körper gerundet ; Fühler mässig lang, mit 5 dickeren, etwas flascheren Endgliedern ; das 2. Glied ist um die Hälfte kürzer als das dritte, welches noch etwas kürzer ist als das vierte ; die folgenden zwei werden immer kürzer. Kopfschild kaum länger als breit, schwach trapezförmig, mit einem seichten Längseindruck. Halsschild elliptisch, mit stumpfwinkligen Ecken vor der Mitte und weit vorgezogener Basis. Flügeldecken mit einem stumpfen Höcker, tief ausgerandeter Basis und eng an den Halsschild anschliessenden Schulterecken ; mit Punktstreifen und viel breiteren Zwischenräumen. Klauen in den Borstenkränzen versteckt, mit einem stumpfen Zahn. Prosternum am Vorderrand gleichmässig abfallend, hinten stark verbreitert.

Typus : *Coptocycla hilaris* Boheman, 1855.

Hovacassis Spaeth, gen. n.

Fühler lang und sehr dünn, bis zur Körpermitte reichend, mit nur drei glatten Basal- und acht nicht dickeren, rauhen, schwach behaarten Endgliedern, das 4. Glied ist schon rauh, aber etwas schwächer behaart als die folgenden ; das 1. und 4. sind je so lang als das 2. und 3. zusammen, welche nur etwa doppelt so lang als dick sind, die dem 4. folgenden sind etwas kürzer, noch dreimal so lang als dick, das letzte länger, beim ♂ schwach sichelförmig und an der Spitze mit langen Haaren. Prosternum zwischen den Hüften breit, der Fortsatz noch breiter, hinten verrundet, ungerandet. Kopfschild trapezförmig, zweimal so lang als breit, ohne Mittelfurche, mit sehr feinen Stirnlinien. Halsschild klein, dreieckig, mit der grössten Breite vor der Mitte. Flügeldecken mit scharfen, vorgezogenen, seitlich weit über den Halsschild hinausragenden Schulterecken und groben Punktstreifen. Seitendach bis hinten sehr breit, die Epipleuren mit weit vor der Spitze die Naht erreichender Innenkante, nach der Spitze fein behaart. Klauen ohne Zahn.

Typus : *Coptocycla discolor* Boheman, 1855.

Floridocassis Spaeth, gen. n.

In Hinsicht der Fühler- und Kopfschild-Bildung der Gattung *Jonthonota* ähnlich, durch die hohe Wölbung, das steile, nicht aufgerandete Seitendach und kürzere Klauen verschieden. Eiförmig, hinten schwach keilförmig verengt, das ♂ kürzer und breiter, das ♀ schmäler und länger, sehr hoch, aber ohne Höcker gewölbt, die äussere Hälfte der Scheibe der Flügeldecken und das Seitendach senkrecht abfallend. Fühler mässig lang, mit 5 von den basalen sehr scharf getrennten, dicht behaarten, viel dickeren Endgliedern, das 2. Glied kurz, das 3. um die Hälfte, das 4. um das doppelte länger, das 5. und 6. kürzer, die Endglieder kaum länger als breit, mit kurzen Ansätzen zu Stirnlinien, das Mittelfeld flach, nicht herausgehoben. Vorderhüften weit von einander abstehend, das Prosternum zwischen ihnen breit, sein Fortsatz kaum breiter; Halsschild vorne wenig, hinten stark gerundet, mit abgestumpften Ecken in der Längsmitte, die Basis beim ♂ durch Andeutung eines Basalzähnchens schwach ausgerandet; Flügeldecken, in beiden Geschlechtern, mit tief ausgerandeter Basis, hier beim ♂ breiter als beim ♀ und dann nach hinten mehr konvergierend, mit vorragenden, verrundeten Schulterecken und feinen, regelmässigen, dicht besetzten Punktstreifen, deren Zwischenräume breiter sind; Seitendach vorn sehr breit, hinten viel schmäler, zerstreut punktiert. Innenkante der Epipleuren ohne Ausrandung, die Naht vor der Spitze erreichend. Klauen kräftig, ohne Zahn, wenig über die Borstenkränze ragend.

Typus: *Coptocycla repudiata* Suffrian, 1868.

Chacocassis Spaeth, gen. n.

Dadurch ausgezeichnet, dass das 3. Fühlerglied nicht länger ist als das 2., das 4. und 5. sind doppelt so lang, die Endglieder beginnen mit dem 6., sind aber weniger an der Behaarung als an der Dicke als solche kenntlich, da die doppelt so dick als die basalen und dicker als lang sind.

Lang-eiförmig, mit parallelen Seiten der Flügeldecken; Kopfschild trapezförmig, wenig länger als breit, mit dreieckigem, nach vorn und zu den Seiten tief, aber ohne scharfe Kanten abfallendem Mittelfeld. Prosternum flach, breit, hinten wenig erweitert. Halsschild elliptisch, mit abgerundeten Ecken nahe der Mitte. Flügeldecken nicht breiter, gleichmässig gewölbt, mit groben, regelmässigen, in weiten Abständen besetzten Punktstreifen und breiteren Zwischenräumen. Das Seitendach fällt fast senkrecht ab; Epipleuren noch an der Spitze breit, die Innenkante erreicht die Naht weit vor der Spitze. Klauen glatt.

Typus: *Coptocycla fuscovittata* Boheman, 1855.

Aporocassida Spaeth, gen. n.

Fühler mässig lang, mit fünf allmählich dickeren Endgliedern, die nicht länger als dick sind, das 3. Glied fast doppelt so lang als das 2. und um die Hälfte länger als das 4. und 5.; Kopfschild trapezförmig, nur wenig länger als breit, schwach gewölbt, ohne Stirnlinien, mit einem, tiefen hufeisenförmigen Eindruck. Vorderrand des Prosternums an der Seite ausgerandet, der Fortsatz verbreitert. Halsschild elliptisch, die verrundeten Ecken in der Längsmitte. Flügeldecken mit gleichmässiger, schwacher Wölbung, parallelen Seiten und feinen Punktreihen. Klauen ohne Zahn.

Typus: *Cassida graphica* Germar, 1824.

Leptocodia Spaeth, gen. n.

Der Kopfschild ist schmal, doppelt so lang als breit, mit seichter, breiter Längsrinne, die Schulterecken sind bis zu dem Vorderrande des Halsschildes vorgezogen, die Endglieder der Fühler sind auffällig verdickt.

Gerundet, mässig gewölbt, mit unbedeutendem Höcker; Fühler nur mässig lang, die Basal- und Endglieder ohne scharfe Abgrenzung, das 2. und 3. Glied gleich lang, die zwei folgenden länger, das 7. doppelt so lang als das 6., die weiteren stark verdickt, nur etwa so lang als dick. Prosternum breit, mit viel breiterem, hinten bogig gerundetem Fortsatz; Halsschild elliptisch, die schmal verrundeten Ecken in der Längsmitte; Flügeldecken mit kaum erkennbaren Punktreihen und breitem, hinten wenig verschmälertem Seitendach; die Innenkante der Epipleuren erreicht die Naht weit vor der Spitze. Klauen ohne Zahn.

Typus: *Coptocycla luctifera* Boheman, 1855.

Aidoia Spaeth, gen. n.

Sehr wenig gewölbt, gerundet-subtriangulär; Kopfschild trapezförmig, doppelt so breit als lang, vorn breit abgestutzt und sowie an der Seite schräg abfallend; Fühler lang, dünn, die schon mit dem 4. Gliede beginnenden Endglieder behaart, kaum dicker, alle mehr als doppelt so lang als dick, das 3. Glied das längste, doppelt so lang als das fast kugelige 2.; Prosternum schmal, der rhombisch erweiterte Fortsatz fällt an der Seite schwach ab; Halsschild sehr klein, subtriangular, vorn kaum gerundet, hinten aussen weit vorgezogen, die schmal abgerundeten Ecken liegen in der Querlinie des Vorderrandes; Flügeldecken viel breiter, ihre Basis ausgerandet, die verrundeten Schulterecken vorgezogen und auch seitlich weit abstehend, die Scheibe mit ganz schwachen, undeutlichen Punktreihen und von der Unterseite durchscheinender Zeichnung; Seitendach vorn sehr breit, hinten sehr verschmälert, flach; die Innenkante der Epipleuren trifft die Naht vor der Spitze; Klauen ohne Zahn, dünn, über die Borstenkränze ragend.

Typus: *Coptocycla nubilosa* Boheman, 1855.

Coptocyclella Hincks, subgen. n.

This subgenus is distinguished from the other (subgenera of *Coptocycla* (p. 341–342) as follows:

The inner base of claws smooth, not striated. Pronotum with anterior and posterior margins more or less equally rounded, its widest part being in or near the middle; angles rounded or feebly obtuse. Distal segments of antennae pubescent and thickened from the seventh segment onwards (in *C. fastidiosa* Boheman, only, from the sixth).

Type: *Cassida adamantina* Germar, 1824.

Bradycassis Spaeth, gen. n.

Umriss eiförmig oder gerundet, Oberseite gleichmässig gewölbt, Fühler kurz, mit fünf dickeren, meist kurzen Endgliedern, das 2. Glied das kürzeste. Prosternum vorn ohne seitliche Ausrandung, der Fortsatz nicht verbreitert. Halsschild elliptisch, vorn mehr gerundet, mit der grössten Breite daher hinter der Mitte. Flügeldecken kaum breiter. Klauen gezähnt.

Typus: *Coptocycla drewseni* Boheman, 1855.

The following additional South American species belong to this genus: *Metriona romani* Spaeth, 1931, *Cassida immersa* Spaeth, 1909, *Metriona sandaricina* (Boheman, 1862), *M. globulipennis* Spaeth, 1926, *M. piagularis* Spaeth, 1926, *M. rudis* Spaeth, 1926, *M. sordescens* Spaeth, 1926, and probably *Coptocycla globosa* Boheman, 1855.

Helocassis Spaeth, gen. n.

Fühler lang, mit fünf von den basalen scharf geschiedenen Endgliedern, die nicht dicker als die basalen, mehr als doppelt so lang als dick und so lang als die einzelnen Glieder 4 bis 6 sind; das 2. Glied ist kurz, das 3. kaum doppelt so lang, die drei folgenden viel länger, etwa dreimal so lang als dick. Kopfschild etwas schmäler als lang, vorn verrundet, flach, glatt, ohne Stirnlinien. Der Halsschild ist unterseits über dem Kopfe gleichmässig gewölbt, zu dessen Aufnahme nicht, wie sonst oft, schwach ausgehöhlt, so dass die Augen nach der Seite frei sind. Prosternum mit tiefer gelegenem, am Ende verrundetem und in eine Ausrandung der Mesosternums eingepassten Fortsatz, hinter dem Vorderrande mit einer Querrinne. Halsschild breit elliptisch, mit der grössten Breite in der Längsmitte und sehr breit gerundeten Seiten. Flügeldecken an der Basis tief ausgerandet, mit weit vorgezogenen, ziemlich scharfen Schulterecken, fast gleichmässiger wölbung kaum bemerkbarem Buckel und nach vorne gerade, hinter der Höckerstelle konvex abfallender Profillinie ; die Punktstreifen sind grob, inner tiefer, ihre Zwischenräume schmäler als sie selbst. Seitendach flach ausgesbreitet, bis zur Spitze breit, undeutlich runzelig punktiert. Die Innenleiste der Epipleuren trifft die Naht weit vor der Spitze. Die Tarsen sind breit, ihr 3. Glied doppelt so breit als lang ; das Klauenglied ist am Ende Zahnförmig erweitert, die Klauen selbst, ohne Zahn ; sie überragen kaum die Borstenkränze.

Typus : *Coptocycla flexuosa* Boheman, 1855.

Chaerocassis Spaeth, subgen. n.

Beim ♂ ist an den Mittel- und Hinterbeinen die äussere Klaue ohne Zahn, die übrigen Klauen sind wie auch alle beim ♀ gezähnt ; Flügeldecken gleichmässig gewölbt, aussen auf der Scheibe mit einem dunkelfärbigen Bogen, dessen beide Enden meist auf das Seitendach reichen. Unterseite des Körpers mit Ausnahme der Beine und der Abdominalrandungen bei allen Arten schwarz.

Typus : *Coptocycla marculenta* Boheman, 1855.

Other species belonging to this subgenus are : *Coptocycla annexa* Boheman, 1855, *C. emarginata* Boheman, 1855, *C. purpurata* Boheman, 1855, and *C. ormondensis* Blatchley, 1926.

Tetracassis Spaeth, gen. n.

Fühler lang und dünn, mit 7 wenig deutlich von den basalen abgegrenzten Endgliedern, die nicht dicker als jene und alle mehr als doppelt so lang als dick sind, nur das 8. etwas kürzer ; das 2. ist kaum halb so lang als das 1, das 3. und 4. sind um die Hälfte länger, aber kürzer als die folgenden. Kopfschild trapezförmig, so lang als breit, mit dreieckigem, herausgehobenem, glattem Mittelfeld ; Prosternum mit breitem, rhombischem Fortsatz. Halsschild klein, fastdreieckig, vorn wenig gerundet, die verrundeten Ecken vor der Mitte. Flügeldecken doppelt so breit, mit bis zur Längsmitte des Halsschildes vorgezogenen, scharfen Schulterecken, stumpfem Höcker und dahinter schwach ausgerandeter Profillinie ; die regelmässigen Punktstreifen werden von glatten Beulenflecken unterbrochen. Die Innenkante der Epipleuren ist am Ende ausgerandet, erreicht die Naht noch vor der Spitze. Alle Klauen mit grossem, lappenförmigem Zahn.

Typus : *Metriona lyra* Spaeth, 1898.

5. SUMMARY.

The generic and subgeneric names hitherto used in the Cassidinae are listed. Types are selected where necessary and previous designations are indicated. Some new genera, subgenera and species mostly described by the late Dr. Franz Spaeth are included. A key to the tribes of the Cassidinae is given.

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